Regeneration dynamics and coexistence of two dioecious tree species, *Podocarpus nagi* and *Neolitsea aciculata*

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Acknowledgements

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Contents

Chapter 1

Introduction

Species coexistence in plant communities has been a considerable subject of ecological research (e.g. Whittaker 1965, 1970; Grubb 1977; Silvertown & Lovett Doust 1993; Tilman 1994). Classical theory offered that every species in a community must occupy a different niche for the coexistence (Hutchinson 1959; MacArthur 1972; Whittaker 1970). Plant ecologists have remarked interspecific differentiations in resource utilization life form, phenology, and requirements for physicochemical characters of habitats as factors that enable plant species to occupy different niches [see reviews by Grubb (1977) and Silvertown & Lovett Doust (1993)]. However, in fact, almost all plants need light, carbon dioxide, water and same mineral nutrients, and numerous species with similar life-form, phenology, and habitat preference coexist in plant communities.

Grubb (1977, 1986) considered that the regeneration process, which was first discussed in general terms by Watt (1947), was important to explain coexistence mechanisms in plant communities and proposed the concept of the regeneration niche. When any one plant individual dies, a gap is created and competition for a gap among plant species occurs. A gap is ultimately occupied by a new plant. It is a crucial point whether a plant that occupy a gap is of the same species as died or not. Grubb (1977) emphasized the importance of this replacement process for understanding species richness in plant communities and suggested that, if species A tends to oust species B, necessary conditions were either the creation of a gap which favors the establishment of B more than A or the creation of a gap at a place where B has propagules and A has not. Grubb (1977) listed factors creating gaps in a forest; fire, cyclone, constant winds, and the fall of single trees or branches. These factors destroy the forest structure and change environmental conditions suddenly (i.e. disturbance, Sprugel 1976; Runkle 1981; Romme 1982; White & Pickett 1985). Especially, a canopy gap, which is caused by a relatively small scale disturbance, has been studied as an important factor on the regeneration of many forest types, tropical rain forests (Brokaw 1985; Hubell & Foster 1986), temperate evergreen forests (Naka 1982; Yamamoto 1992), temperate deciduous forests (Runkle 1985; Nakashizuka 1987, Yamamoto 1989).

On the other hand, the forest structure could be changed gradually as the results of biological interactions among plants (Janzen 1970; Connell 1971; Pielou 1977; Greig-Smith 1979; Woods 1984; Callaway 1992; Silvertown & Wilson 1994). The spatial

pattern of plants reflected the biological interactions throughout the regeneration processes, i.e., production of propagules, dispersal of propagules, germination, establishment, growth and mature. In a dispersal phase, the location of parent plants and their seed dispersal ability initially determine the spatial pattern of their offspring (Augspurger 1983; Hoppes 1988; Houle 1992) and eventually affect the spatial structure of populations (Hubbell 1979; Abbott 1984; Sterner *et al.* 1986; Armesto *et al.* 1991). The spatial pattern of plant species appears to be affected by their means of seed dispersal (Hubbell 1979; Briggs & Gibson 1992). Small dispersal distances could explain the clumped distribution of plants (Prentice & Werger 1985; Sterner *et al.* 1986; Hatton 1989), whereas plants with large dispersal ability showed less clumped distribution (Briggs & Gibson 1992).

In a post-dispersal phase, the offspring interact with the neighbouring plants through the competition to acquire the resources, i.e., light, water, and nutrients. The competition among plants affects the species composition and population structure of each species in a plant community (Greig-Smith 1979; Fowler 1986). In monospecific stands, more regular spatial patterns have often been reported with an increase in plant size (or age) and such a shift has been explained to be induced by intraspecific competition (Laessle 1965; West 1984; Kenkel 1988; Kenkel *et al.* 1997). Similar shifts in spatial patterns have also been reported in multi-species stands (Christensen 1977; Phillips & MacMahon 1981; Sterner *et al.* 1986; Duncan 1991; Fulé & Covington 1998). In multi-species stands, both intra- and interspecific competitions should be considered (Duncan 1991; Nakashizuka & Kohyama 1995 ; Hara *et al.* 1995; Kubota & Hara 1995, 1996; Peterson & Squiers 1995a,b).

By interspecific competition, the habitat of species with inferior competitive ability was restricted to the sites where density of superior competitor was low (Gurevitch 1986; Haase *et al.* 1997; Bockelmann & Neuhaus 1999). Hart *et al.* (1989) reported that the superior competitive ability of species with large seeds and high shade tolerance resulted in the formation of monodominant stands within a species-rich tropical forest. Frelich *et al.* (1993) and Frelich *et al.* (1998) reported a mixed-species forest consisting of mono-specific patches and that interspecific competition was responsible for the patch formation.

Formation of the sites where density of superior competitor was low can facilitate the species coexistence. The coexistence of species competing with each other for gaps is facilitated by a trade-off between relative competitive and dispersal ability, i.e., superior competitors tend to have inferior dispersal abilities and vice versa (Skellam

1951; Hutchinson 1975; Hanski & Ranta 1983; Shmida & Ellner 1984; Marino 1991; Tilman 1994). Coexistence occurs because species with inferior competitive ability but sufficiently wide dispersal ability persist in site not occupied by superior competitors. In circumstances where superior competitors with narrow dispersal range are spatially aggregated, inferior competitors can coexist by creation of spatial refuge from superior competitor (Silvertown & Lovett Doust 1993). The regeneration niche (Grubb 1977) for inferior competitor can be created by the spatial population structure of superior competitor without any disturbances.

However, spatial patterns and population dynamics of plants have been studied in hermaphrodite or monoecious species, of which all parent plants can produce seeds. In the case of dioecious species, not all parent plants produce seeds. When the number of male and female plants in a dioecious population is the same, only a half of the parent plants contribute to seed dispersal to determine the spatial pattern of offspring. The decrease in the number of seed sources in dioecious species can result in a greater spatial heterogeneity of offspring density than in hermaphrodite or monoecious species. The spatial heterogeneity of plant density is influential to the community structure and dynamics (Greig-Smith 1979; Peterson & Squiers 1995a, b). Dioecy may facilitate the formation of the spatial refuge for the species coexistence where the density of the superior competitor was low.

The dioecy leads us to suspect that the population structure and dynamics are different from those observed in hermaphrodite or monoecious species. The studies on dioecious species have focused on sex ratio (Opler & Bawa 1978; Allende & Harper 1989; Vasiliauskas & Aarssen 1992), secondary sex characteristics (Lloyd & Webb 1977; Hoffmann & Allende 1984; Lovett Doust & Lovett Doust 1988) and spatial segregation of the sexes (Freeman *et al*. 1976; Grant & Mitton 1979; Bierzychudek & Eckhart 1988). However, the effects of the dioecy-induced characteristics on the spatial structure and dynamics of populations have not been studied in detail yet. There are several studies on the spatial pattern and dynamics of dioecious species, but few studies consider the dioecy (but see Gibson & Menges 1994). The dioecy-induced effects on the intra- and interspecific competition and species coexistence in a forest community have not been studied.

Objectives of the study

The aims of this study are to elucidate the regeneration dynamics of a forest community

which is dominated by two dioecious tree species, *Podocarpus nagi* (Thunb.) Zoll. et Moritz (Podocarpaceae) and *Neolitsea aciculata* (Blume) Koidz. (Lauraceae), and to discuss the dioecy effects on the coexistence mechanism of the two species. *Podocarpus nagi* has a higher shade tolerance than *N. aciculata* (Aiba & Kohyama 1997). *Podocarpus nagi* whose seeds are dispersed by gravity alone has a narrower seed dispersal range than *N. aciculata* whose seeds are dispersed by birds. The author focused on their competitive ability, sex expression and seed dispersal ability to explain the dioecy-induced effects on the regeneration dynamics and coexistence mechanism of the two species.

The following chapters of this dissertation will provide a detailed explanation of the results of various researches conducted. An overview of the content of each chapter is shown below:

• In Chapter 2, dioecy-induced spatial patterns of a forest community were detected. The spatial interactions (attraction or repulsion) between juvenile plants (seedlings and saplings) and parent plants (male and female trees) were analysed to detect the effects of dioecy on the spatial patterns of a population. The dependency of the dioecy effects on a seed dispersal ability was evaluated by comparing the degrees of the juvenile-parent interactions in the *P. nagi* population (small dispersal ability) with those in the *N. aciculata* population (large dispersal ability). The spatial interactions (attraction or repulsion) between the two species were analysed to detect the evidence of dioecy effects on the regeneration and coexistence of the two species.

• In Chapter 3, sex-related population structures of *P. nagi*, i.e., sex ratio and spatial patterns of males and females were analysed and the driving force of the sex-related population structures of *P. nagi* was evaluated. The sex ratios at various size classes were compared to examine the size-dependency of sex ratio. The growth rates were compared between males and females at various size classes to examine the sex- and size-dependency of growth rates. The intensities of competition within sexes and between sexes were evaluated by analysing neighbouring effects on the growth rate. The spatial interactions (attraction or repulsion) between males and females were analysed to detect the evidence of sex-dependent growth rates reflected on the spatial patterns of the *P. nagi* population.

• In Chapter 4, spatial pattern formation in the forest community was explained by the measurements of growth, survival and mortality of *P. nagi* and *N. aciculata* trees. The neighbouring effects on the growth rate of trees were analyzed to evaluate the relative importance of intra- and inter-specific competition on the pattern formation. The changes

in the spatial patterns by mortality were analysed to detect the evidence of the pattern formation reflected on the *P. nagi* and *N. aciculata* community.

• In Chapter 5, a theoretical analysis for the coexistence mechanism of the two species was conducted by a matrix model incorporating competitive ability, seed dispersal ability and dioecy of the two species. The model hypothesized that seed dispersal in *P. nagi* is limited to the area around female trees; the density of young plants of *P. nagi* become high in the area around female trees but low in the area around male trees; seed dispersal of *N. aciculata* is sufficient to occur at any point within the forest; and the regeneration of *N. aciculata* is facilitated where *P. nagi* plants are uncommon and competition is therefore less intense.

Focal species

Podocarpus nagi (Thunb.) Zoll. et Moritz. (Podocarpaceae) is a dioecious gymnosperm, a native of southwestern Japan, Taiwan, and southern China. The shade tolerance is high (Kohyama & Grubb 1994) to 'extremely high' (Suganuma & Kawai 1978). The seeds are round and 10–15 mm in diameter and are dispersed by gravity.

Neolitsea aciculata (Blume) Koidz. (Lauraceae) is a dioecious angiosperm, growing in warm-temperate forests of southwestern Japan. The shade tolerance is high (Kohyama & Grubb 1994). The fruit is an ellipse about 10 mm in length and contains one seed. The seeds are dispersed by birds (Nakanishi 1996; Noma & Yumoto 1997).

Study site

The study forest was located on a low hill, Mt. Mikasa (294 m alt., 34° 41'N, 135° 51'E), Nara City, Japan. The forest is adjacent to Nara Park, where the Sika deer (*Cervus nippon* Temminck) population has been conserved as holy animals by the Kasuga Shinto Shrine established in the early eighth century. The population density of deer around the forest has been constant at about 1000 head since the 1960's (the Society of Deer Conservation, Nara 1994; Ohmae *et al.* 1996). The deer feed freely and have been influential to the structure and species composition of vegetation in and around the forest.

The Nara Meteorological Station (104 m alt.) recorded an average annual temperature (1961–1990) of 14.4°C and precipitation (1961–1990) of 1354.7 mm. The natural vegetation in this area is an evergreen broad-leaved forest (Suganuma & Kawai 1978). The preserved forest at Mt. Kasuga adjacent to Mt. Mikasa is dominated by

evergreen oak species (Naka 1982). The vegetation around Mt. Mikasa is, however, altered by the browsing pressure of abundant deer and characterized by unpalatable species, such as *P. nagi*, *N. aciculata*, *Pieris japonica* (Thunb.) D. Don and *Illicium religiosum* Sieb. et Zucc. (Koshimizu *et al.* 1971; Suganuma & Kawai 1978; Shimoda *et al.* 1994; Ohmae *et al.* 1996). These species escaped from the browsing pressure by a chemical defense mechanism (Takatsuki 1989).

At Mt. Mikasa, the deer population has been influencing the altered vegetation consisted of unpalatable species. Among these species *P. nagi* is the most abundant. *Podocarpus nagi* is not a native species in this area. The population of *P. nagi* at Mt. Mikasa is believed to be derived from trees transplanted about 1000 years ago around the Kasuga Shinto Shrine located at a foot of Mt. Mikasa (Suganuma & Kawai 1978). The *P. nagi* population has been expanding its distribution from the foot to the peak of Mt. Mikasa. Koshimizu *et al.* (1971) and Suganuma & Kawai (1978) considered that *P. nagi* replaced all the native tree species by its superior shade tolerance. However, several native species grow mixed. *Neolitsea aciculata* is especially abundant. We consider that *N. aciculata* is a codominant species with *P. nagi*. In a natural evergreen forest, Yakushima Island, southern Japan, the two species are major components of the forest canopy (Aiba & Kohyama 1997). *Podocarpus nagi* is superior in shade tolerance, while *N. aciculata* is superior in growth rate in improved light conditions (Aiba & Kohyama 1997).

Chapter 2

Dioecy-induced spatial patterns of two codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*

Introduction

Analysis of the spatial patterns of plants is a useful approach to detect the interactions among plants, both intra- and interspecific, because the spatial patterns often preserve the evidence of their interactions (Pielou 1977; Greig-Smith 1979; Silvertown & Wilson 1994). Since plants are sessile, the location of parent plants and their seed dispersal ability initially determine the spatial pattern of their offspring (Augspurger 1983; Houle 1992) and eventually affect the spatial structure of populations (Hubbell 1979; Sterner *et al.* 1986; Armesto *et al.* 1991). The offspring interact with the neighbouring plants through competition for limiting resources, i.e., light, water, and nutrients. The growth and mortality of both offspring and neighbouring plants are influenced by their distance, local density, size, and species composition (Black 1960; Harper 1977; Mack & Harper 1977; Antonovics & Levin 1980; Weiner 1984; Kenkel 1988; Condit *et al.* 1994; Peterson & Squiers 1995a, b; Kenkel *et al.* 1997).

Spatial patterns of plants have been studied in hermaphrodite or monoecious species, of which all parent plants can produce seeds. In the case of dioecious species, when the number of male and female plants in a population is the same, only half of the parent plants contribute to seed dispersal. The decrease in the number of seed sources in dioecious species can result in a greater spatial heterogeneity of offspring density than in hermaphrodite or monoecious species. The spatial heterogeneity of plant density is influential to the community structure and dynamics (Greig-Smith 1979; Peterson & Squiers 1995a, b). However, the effects of dioecy on the spatial structure of populations have not been studied in detail yet. There are several studies on the spatial pattern of dioecious species, but few studies of them consider the dioecy (e.g. Gibson & Menges 1994).

Here, we analysed the spatial patterns of a forest community dominated by two dioecious tree species, that have different seed dispersal modes and shade tolerances. We have three purposes: (1) to detect the effects of dioecy on the spatial patterns of the two

species, (2) to evaluate the difference of the dioecy effects on the spatial patterns between the two species, and (3) to examine whether the dioecy affects the interactions of the two species.

One of the two species is *Podocarpus nagi* (Thunb.) Zoll. et Moritz. (Podocarpaceae). The seeds of *P. nagi* are dispersed by gravity alone. The other is *Neolitsea aciculata* (Blume) Koidz. (Lauraceae). *Neolitsea aciculata* is a bird-dispersed species. Thus the seed dispersal range of *P. nagi* is narrower than that of *N. aciculata*. The narrow seed dispersal is expected to reveal the heterogeneity of spatial distribution of the offspring caused by dioecy, while the wide seed dispersal may moderate the spatial heterogeneity.

The coexistence of species is facilitated by a trade-off between relative competitive and dispersal ability, i.e., superior competitors have inferior dispersal abilities and vice versa (Skellam 1951; Hutchinson 1975; Hanski & Ranta 1983; Marino 1991). *Podocarpus nagi* is superior in shade tolerance while *N. aciculata* is superior in seed dispersal ability. The two species were codominant in our study site. The trade-off between shade tolerance and seed dispersal ability may promote the coexistence of *P. nagi* and *N. aciculata*. Furthermore, the spatial heterogeneity of *P. nagi* caused by dioecy may also influence the behaviour (establishment and growth) of *N. aciculata*. We tried to examine the probability of coexistence of the two species through the dioecy effects.

Methods

Field methods

In 1988, a 40 m width × 370 m length (1.48 ha) plot was established from the foot to the peak of Mt. Mikasa, along which the *P. nagi* population was considered to be expanding its distribution. The plot was divided into 5 m × 5 m quadrats. Within each quadrat, the x and y coordinates to the centre of all plants larger than 5 cm in stem diameter at breast height (d.b.h., 130 cm above ground level) were mapped, and their species and size were recorded. The total number of *P. nagi*, *N. aciculata* and other species were 1227, 1568 and 263, respectively. *Podocarpus nagi* and *N. aciculata* are codominant in the plot. Although the biological invasion by *P. nagi* is an interesting phenomenon, in this paper we focused on the effects of dioecy on spatial patterns and the coexistence mechanism of *P. nagi* and *N. aciculata*. For this purpose, we selected the bottom 40 m × 40 m part of

the whole plot to carry out intensive investigation, because we considered that in the bottom part, sufficient time had elapsed after *P. nagi* invasion and spatial patterns observed were highly representative for detecting the eventual results of interspecific interaction between *P. nagi* (invader) and *N. aciculata* (native species). In the upper part of the plot, *P. nagi* had invaded recently and interspecific interaction might still be in process. The comparison between the density of *P. nagi* trees larger than 5 cm d.b.h. in the 40 m × 370 m plot (829/ha) and that in the bottom 40 m × 40 m part (1663/ha) suggested the earlier invasion of *P. nagi* in the bottom part. In the 40 m × 40 m plot, from July to August 1993, all plants including one-year old seedlings were mapped, and their species and size were recorded.

For each plant larger than 5 cm in d.b.h., reproductive organs were observed using binoculars and sex was discriminated. The degree of reproductive production in each tree was recorded in five classes. For *P. nagi*, strobili were observed in 1989, 1991, 1993 and 1995. For *N. aciculata*, inflorescence was observed in 1989 and every year from 1991 to 1997. In 1991, *P. nagi* produced many seeds. To observe the seed dispersal pattern of *P. nagi*, the plot was divided into 1 m × 1 m quadrats. Between May and July 1992, when most seeds had fallen and had not germinated, the number of seeds of *P. nagi* on the forest floor was counted within each quadrat.

Data analysis

The life stage of each species was distinguished on the basis of age and size. The population of *P. nagi* was divided into four stages, i.e., one-year old seedlings (1-yr seedlings), saplings (d.b.h. < 5 cm), small trees (5 ≤ d.b.h. < 30 cm) and large trees (d.b.h. ≥ 30 cm). The population of *N. aciculata* was divided into three stages, i.e., 1-yr seedlings, saplings (d.b.h. < 5 cm) and large trees (d.b.h. ≥ 5 cm). Wider size intervals were used for *N. aciculata* than *P. nagi* because sample size was too small for tests if finer divisions were used. For both species, large trees were further divided into male, female and unsexed trees. The unsexed trees lacked reproductive organs during observations.

Univariate spatial patterns of plants were analysed using Ripley's $K(t)$ function (Ripley 1977). The function $\lambda K(t)$ (λ = intensity) is defined as the expected number of plants within distance t of an arbitrary plant. The unbiased estimate of $K(t)$ is defined as

$$K(t) = n^{-2}|A|\sum_{i \neq j}\sum w_{ij}^{-1} I_t(u_{ij}), \quad (1)$$

where n is the number of plants in a plot A; |A| denotes plot area; u_{ij} is the distance between ith plant and jth plant in A; $I_t(u)$ is equal to 1 if $u \leq t$ and 0 otherwise; w_{ij} is the proportion of the circumference of a circle with centre at ith plant and radius u_{ij} that lies within A; and summation is for all pairs of plants not more than t apart (Ripley 1977; Diggle 1983; Upton & Fingleton 1985).

A square-root transformation of $K(t)$ suggested by Besag (1977) is easier to use:

$$L(t) = [K(t)/\pi]^{1/2} - t, \quad (2)$$

A value of $L(t) = 0$ indicates that the spatial pattern at distance t is random. Values of $L(t) > 0$ indicate clumped distribution, whilst values of $L(t) < 0$ indicate regular distribution.

Spatial interactions between two groups of plants were analyzed using the bivariate function $L_{12}(t)$, a transformation of function $K_{12}(t)$ (Lotwick & Silverman 1982):

$$L_{12}(t) = [K_{12}(t)/\pi]^{1/2} - t, \quad (3)$$

The function $K_{12}(t)$ is a generalization of the function $K(t)$ to a bivariate point process. $L_{12}(t) = 0$ indicates that the two groups are spatially independent, values of $L_{12}(t) > 0$ indicate positive association (attraction) and values of $L_{12}(t) < 0$ indicate negative association (repulsion).

Significance of both functions was determined with Monte Carlo simulations (Besag 1977; Besag & Diggle 1977; Marriott 1979). For the univariate spatial pattern of plants, the null hypothesis is complete spatial randomness. For the bivariate spatial interactions between two groups, the null hypothesis is spatial independence. Ninety-five per cent confidence envelopes were defined as the highest and lowest values of $L(t)$ or $L_{12}(t)$ for each spatial scale found in 19 analyses of random point distributions. Ninety-nine per cent confidence envelopes require 99 simulations. See earlier uses of $L(t)$, $L_{12}(t)$ and Monte Carlo simulations in West (1984), Prentice & Werger (1985), Sterner *et al.* (1986), Kenkel (1988, 1993), Hatton (1989), Rebertus *et al.* (1989), Duncan (1991), Andersen (1992), Peterson & Squiers (1995b), Haase (1995), Kenkel *et al.* (1997) and Fulé & Covington (1998).

In this study 'degree' and 'scale' of clumping are defined following Rebertus *et al.* (1989). 'Degree' refers to the magnitude of the deviation from randomness. 'Scale' refers to pattern at a particular radius around each plant. The distance with maximum clumping value (peak) suggests the radius of clumps.

Results

Species composition

The plot contained a total of 25 woody species. *Podocarpus nagi* and *Neolitsea aciculata* accounted for 79% and 16% of all 7225 plants, respectively (Table 2.1). The other 23 species occupied only 5%. Of 368 plants larger than 5 cm d.b.h, *P. nagi*, *N. aciculata* and other 12 species accounted for 72%, 20% and 8%, respectively (Table 2.1).

Table 2.1. Number of plants of woody species in the 40 m × 40 m plot at Mt. Mikasa, Nara City, Japan

Species	Number		
	d.b.h. < 5 cm	d.b.h. ≥ 5 cm	Total
Podocarpus nagi	5442	266	5708
Neolitsea aciculata	1062	73	1135
Other woody species			
Evergreen broad-leaved (10 spp.)	292	13	305
Deciduous broad-leaved (5 spp.)	12	6	18
Evergreen conifers (2 spp.)	6	2	8
Climbers (6 spp.)	43	8	51
Total	6857	368	7225

Sex ratios of Podocarpus nagi *and* Neolitsea aciculata

The sex ratio of large *P. nagi* trees did not differ from the null hypothesis of a 1:1 ratio (Table 2.2). However, small sexed trees (40% of a total) were significantly male biased ($P < 0.01$) with a male/female ratio of 1.90. The sex expression of 133 out of 266 trees larger than 5 cm in d.b.h. was not determined. The number of unsexed trees tended to decrease with increasing tree size and all trees larger than 24.2 cm in d.b.h. were sexed. The degree of seed production of smaller female trees was lower than that of larger female trees. Thus the influence of the smaller female trees, which are sexed or unsexed, on the spatial pattern of *P. nagi* population is expected to be small.

There was a significant male dominance in *N. aciculata* ($P < 0.05$, Table 2.2). Of all large *N. aciculata* trees, 22% were female, 45% male, and 33% unsexed. Trees with a higher degree of flower production showed a constant flowering during the 8 years of observation. The seed production of any unsexed trees that had produced seeds before the study period is expected to be less influential on the spatial pattern.

Table 2.2. Number of plants according to each life stage and sex of *Podocarpus nagi* and *Neolitsea aciculata* in the 40 m × 40 m plot at Mt. Mikasa, Nara City, Japan. For plants larger than 5 cm in d.b.h., reproductive organs and sex expression were observed. The chi-square statistic compared the number of male and female plants and was calculated based on the expected 1:1 male to female sex ratio; * $P < 0.05$, ** $P < 0.01$, n.s. $P \geq 0.05$

Podocarpus nagi

Life stage	Total	Male	Female	Unsexed	Male/Female	Chi-square	
One year seedlings	337						
Saplings (d.b.h < 5 cm)	5105						
Small trees (5 ≤ d.b.h. < 30 cm)	220	57	30	133	1.90	8.38	**
Large trees (d.b.h. ≥ 30 cm)	46	24	22	0	1.09	0.09	n.s
Small and large trees (d.b.h. ≥	266	81	52	133	1.56	6.32	*

Neolitsea aciculata

Life stage	Total	Male	Female	Unsexed	Male/Female	Chi-square	
One-year seedlings	197						
Saplings (d.b.h. < 5 cm)	865						
Large trees (d.b.h. ≥ 5 cm)	73	33	16	24	2.06	5.90	*

Seed dispersal of Podocarpus nagi

There were 18646 (11.7 m $^{-2}$) seeds of *P. nagi* in the 40 m × 40 m plot (Fig. 2.1). The highest density was 344 m $^{-2}$. Clumps of seeds were observed under canopies of large female trees. The density of seeds decreased with increasing distance from the centre of the clump, and little seeds were found > 7 m from the centre of the clump (Figs 2.2 and 2.3).

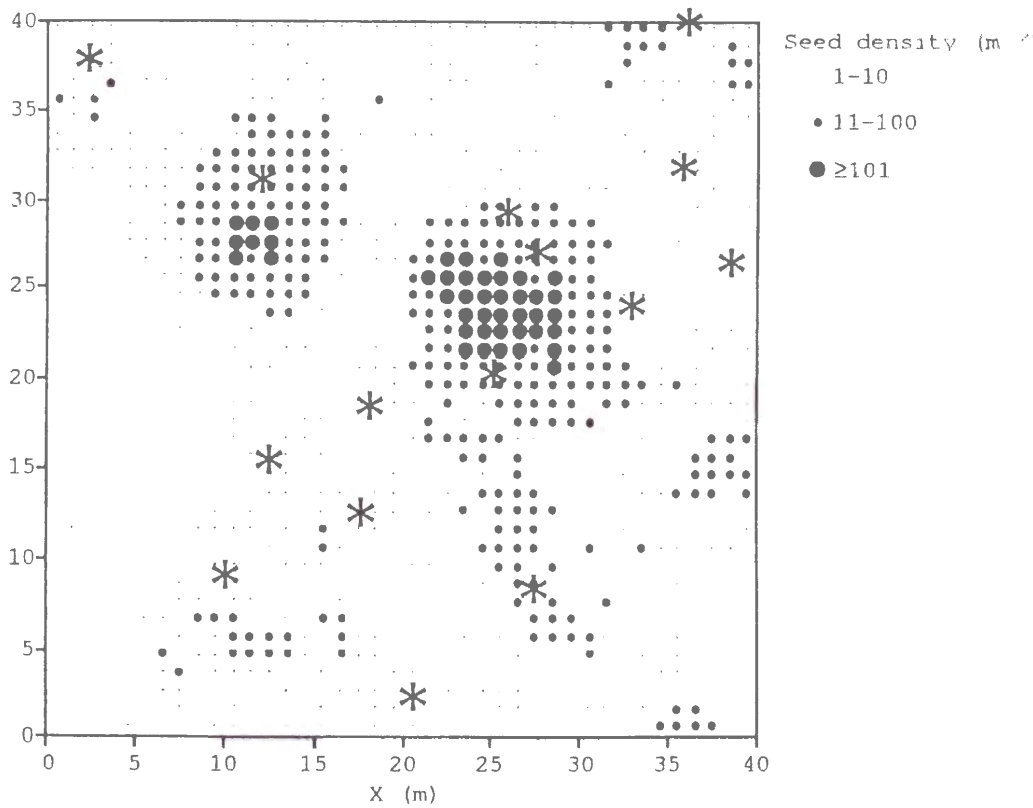

Fig. 2.1. Distribution map of fallen seeds of *Podocarpus nagi* on the forest floor in the 40 m × 40 m plot at Mt. Mikasa, Nara City, Japan. The size of circles indicates the number of seeds in each 1 m × 1 m quadrat. Asterisks indicate locations of stem bases of female trees that had produced seeds in the previous year, 1991.

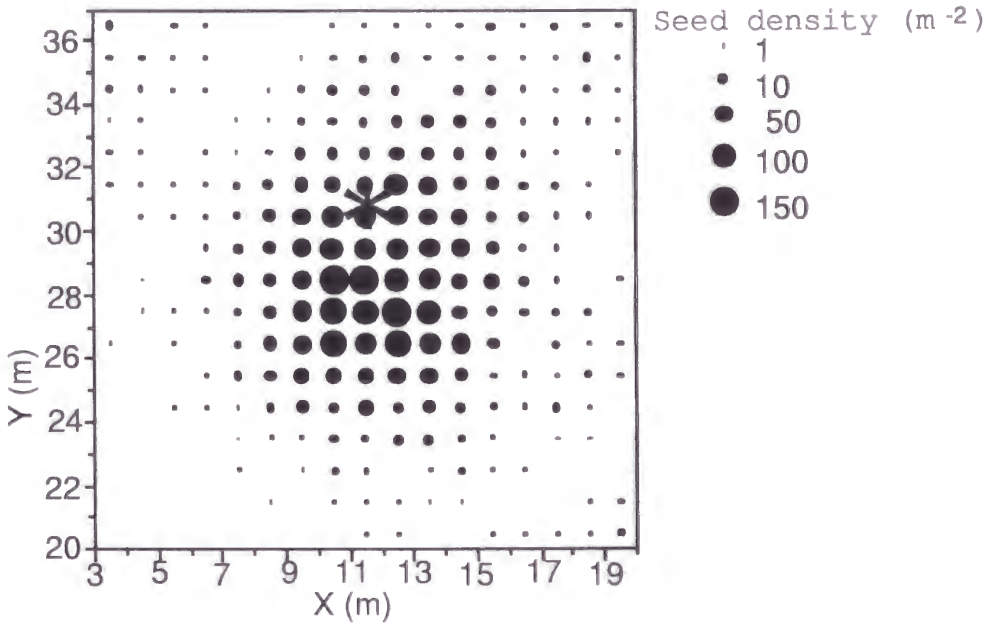

Fig. 2.2. Distribution of fallen seeds of *Podocarpus nagi* in a clump, the centre of which is at x = 11.5 m and y = 28.5 m in Fig. 2.1. The area of each circle is proportional to the number of seeds in each 1 m × 1 m quadrat. The asterisk indicates the location of the stem base of a female tree that produced seeds in 1992.

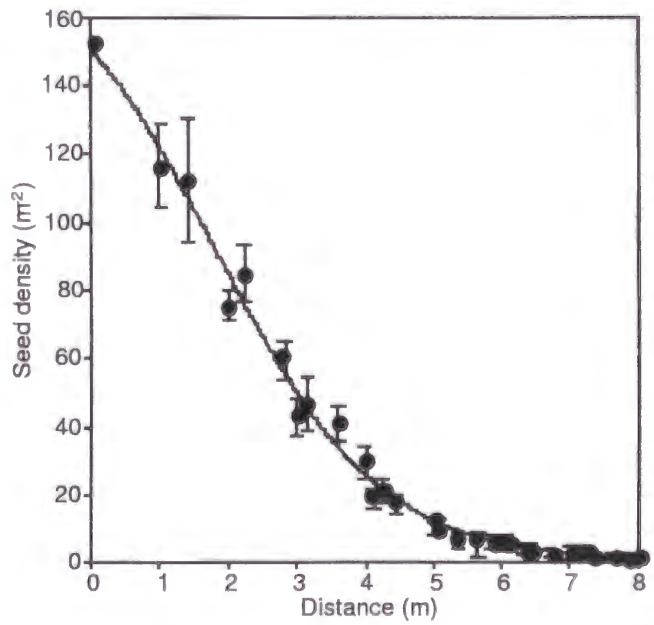

Fig. 2.3. Seed density in relation to the distance from the centre of a seed clump of *Podocarpus nagi* in Fig. 2.2. The mean number of seeds in 1 m × 1 m quadrats located at the same distance from the centre. Bars indicate standard errors. Fitted line; $f(x) = 1/[0.00116\exp(0.843x) + 0.00547]$, r^2=0.989.

Spatial pattern of Podocarpus nagi

Analysis of the spatial distribution of *P. nagi* (Fig. 2.4) showed that 1-yr seedlings and saplings were significantly ($P < 0.01$) clumped at distances of 1–15 m (Figs 2.5a and b). Small trees were significantly ($P < 0.01$) clumped at 2–15 m (Fig. 2.5c). One-yr seedlings were maximally clumped at 5 m. This suggested that clumps of 1-yr seedlings had about a 5 m radii. Sapling and small trees did not show a distinct peak. Magnitude of departure from randomness became smaller in the order of 1-yr seedlings, saplings and small trees, implying that the degree of clumping of plants decreased progressively with increasing plant size. Large trees showed a significant regular distribution at 3 m ($P < 0.05$), 4–6 m ($P < 0.01$) (Fig. 2.5d). The $L(t)$ value of large trees was lowest at 5 m. This suggested that there was a tendency for larger trees not to occur within a 5 m distance of each other.

One-yr seedlings of *P. nagi* showed a significant attraction to large female trees at 5-6 m ($P < 0.05$) and 14–15 m ($P < 0.01$) (Fig. 2.6a), and a significant repulsion from large male trees at 1–4 m ($P < 0.05$) (Fig. 2.6d). Saplings showed a significant attraction to large female trees at 2 m ($P < 0.05$), 3–4 m ($P < 0.01$) and 5 m ($P < 0.05$) (Fig. 2.6b), and a significant repulsion from large male trees at 1 m, 3–4 m ($P < 0.05$) (Fig. 2.6e). Small trees showed no significant departure from independence of large female trees at 1 m, 3–15 m (Fig. 2.6c) and significant repulsion from large male trees at 5–7 m ($P < 0.01$), 8–11 m ($P < 0.05$) and 12-13 m ($P < 0.01$) (Fig. 2.6f). Thus, large female trees were accompanied by a significantly large number of neighbouring 1-yr seedlings and saplings, while there was a tendency for 1-yr seedlings, saplings and small trees not to occur around large male trees.

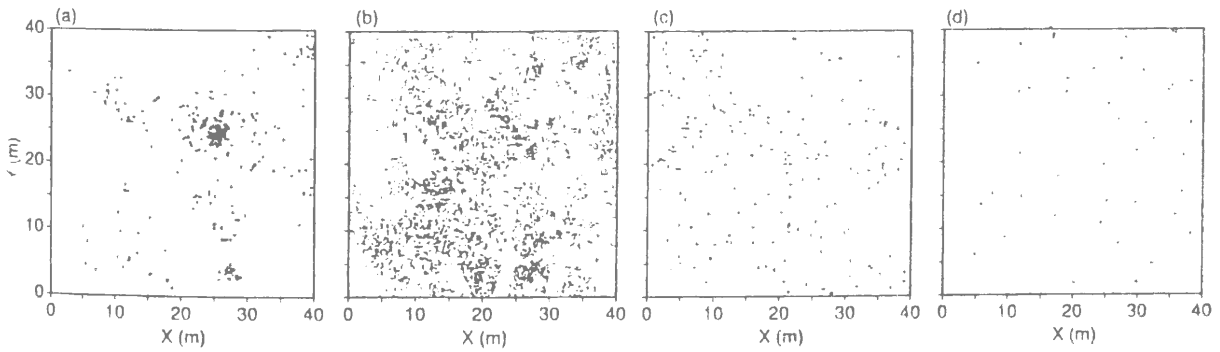

Fig. 2.4. The spatial distribution of the *Podocarpus nagi* population in the 40 m × 40 m plot at Mt. Mikasa, Nara City, Japan: (a) 1-yr old seedlings ($n = 337$), (b) saplings ($n = 5105$), (c) small trees ($n = 220$), (d) large trees ($n = 46$).

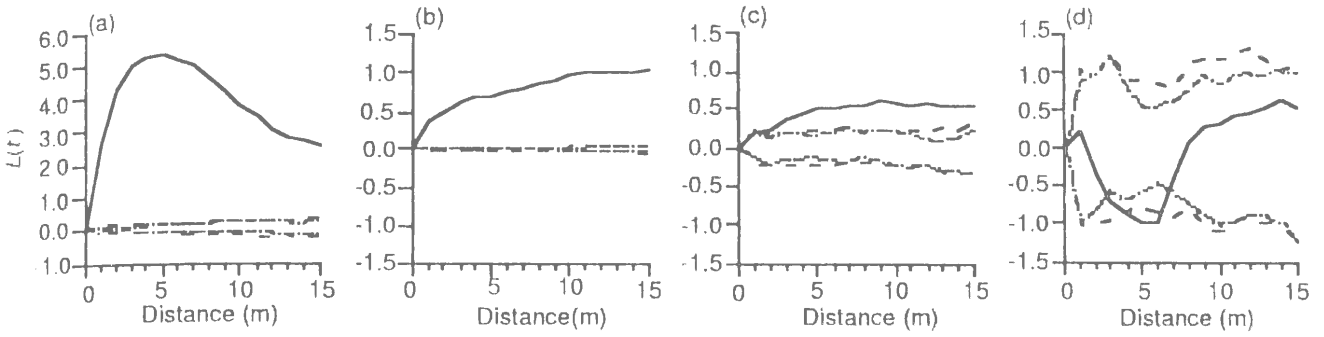

Fig. 2.5. $L(t)$ values for the *Podocarpus nagi* population: (a) 1-yr old seedlings, (b) saplings, (c) small trees, (d) large trees. The solid line shows actual $L(t)$ values for extant plants, dotted lines and broken lines show 95% and 99% confidence envelopes for the pattern expected from a random distribution of plant locations, respectively. Values outside the envelopes indicate significant departure from randomness.

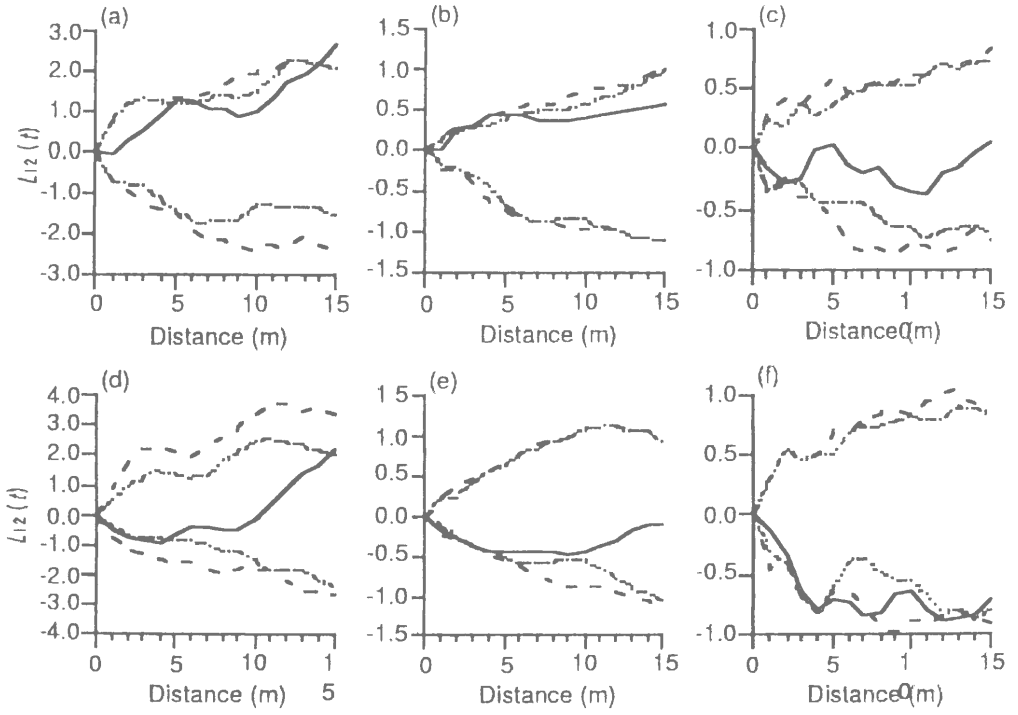

Fig. 2.6. $L_{12}(t)$ values of bivariate distribution of *Podocarpus nagi* population: (a) 1-yr seedlings vs. large female trees, (b) saplings vs. large female trees, (c) small trees vs. large female trees, (d) 1-yr seedlings vs. large male trees, (e) saplings vs. large male trees, (f) small trees vs. large male trees. The solid line shows actual $L_{12}(t)$ values for extant plants, dotted lines and broken lines show 95% and 99% confidence envelopes for the pattern expected from an independent distribution of plant locations, respectively.

Spatial pattern of Neolitsea aciculata

The spatial distribution of *N. aciculata* (Fig. 2.7) was analysed. One-yr seedlings and saplings were significantly clumped at distances of 1–15 m ($P < 0.01$) (Figs 2.8a and b). Large trees were significantly clumped at 1 m ($P < 0.05$) and 2–13 m ($P < 0.01$) (Fig. 2.8c). The pattern of clumping in 1-yr seedlings indicated an indistinct peak at a distance around 9–12 m. Clumps of 1-yr seedlings of *N. aciculata* were indistinct and larger than those of *P. nagi* (Figs 2.5a and 2.8a). Saplings did not show a peak. Large trees indicated a distinct peak at 7 m. Large trees were more distinctly clumped than 1-yr seedlings and the clump radii were smaller than those of 1-yr seedlings.

One-yr seedlings were spatially independent of large female and large non-female (male and unsexed) trees at 1–15 m (Figs 2.9a and c). Saplings were spatially independent of large female trees at 1–15 m (Fig. 2.9b) and showed a significant repulsion at 3-5 m ($P < 0.05$) from large non-female trees (Fig. 2.9d).

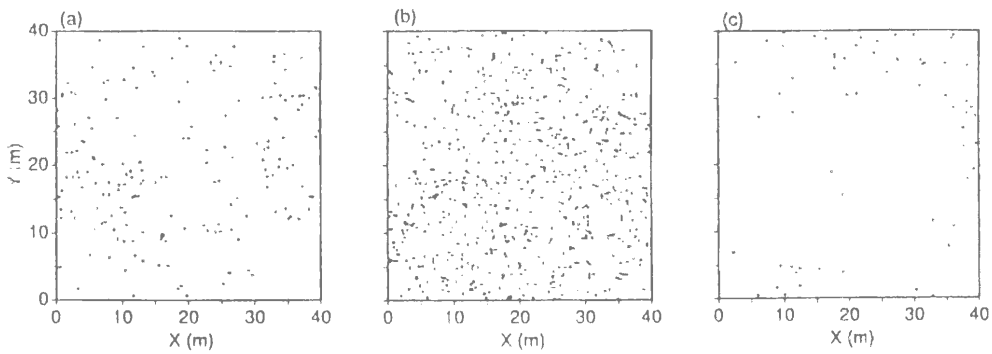

Fig. 2.7. The spatial distribution of *Neolitsea aciculata* population in the 40 m × 40 m plot at Mt. Mikasa, Nara City, Japan: (a) 1-yr seedlings (n = 197), (b) saplings (n = 865), (c) large trees (n = 73).

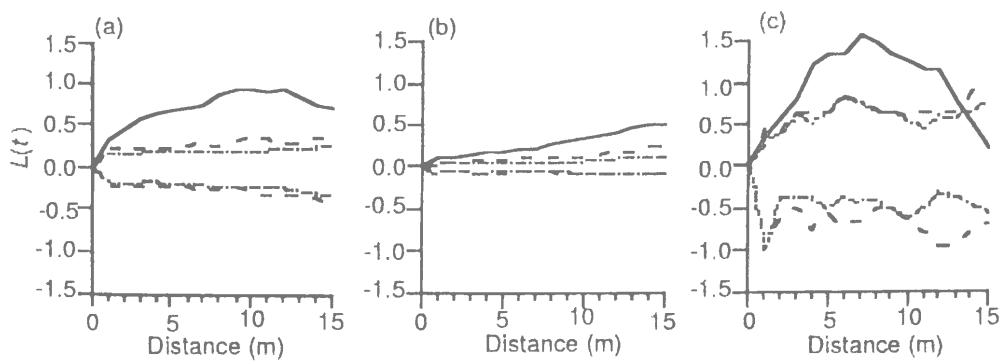

Fig. 2.8. $L(t)$ values of *Neolitsea aciculata* population: (a) 1-yr seedlings, (b) saplings, (c) large trees. Conventions as in Fig. 2.5.

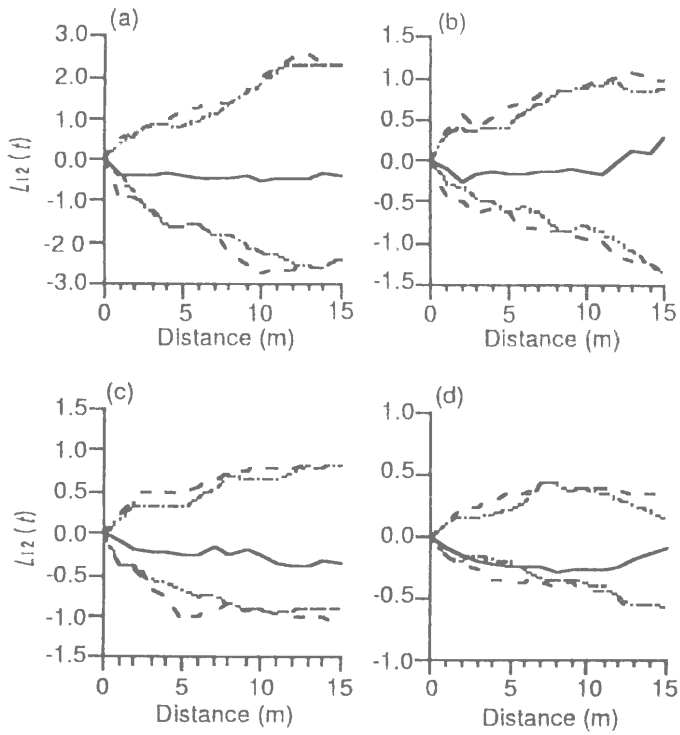

Fig. 2.9. $L_{12}(t)$ values of bivariate distribution *Neolitsea aciculata* population: (a) 1-yr seedlings vs. large female trees, (b) saplings vs. large female trees, (c) 1-yr seedlings vs. large male and unsexed trees, (d) saplings vs. large male and unsexed trees. Conventions as in Fig. 2.6.

Spatial interaction between Podocarpus nagi *and* Neolitsea aciculata

The spatial distribution of *N. aciculata* trees and large male and female *P. nagi* trees was analysed (Fig. 2.10). Bivariate analyses indicated that 1-yr seedlings and saplings of *N. aciculata* were spatially independent of large male and female *P. nagi* trees (Figs 2.11a, b, d and e). Large *N. aciculata* trees showed a significant attraction to large male *P. nagi trees* at distances of 1 m ($P < 0.01$), 3–6 m and 8-11 m ($P < 0.05$) (Fig. 2.11f), and a weak non-significant repulsive tendency from large female *P. nagi trees* at 5–7 m (Fig. 2.11c).

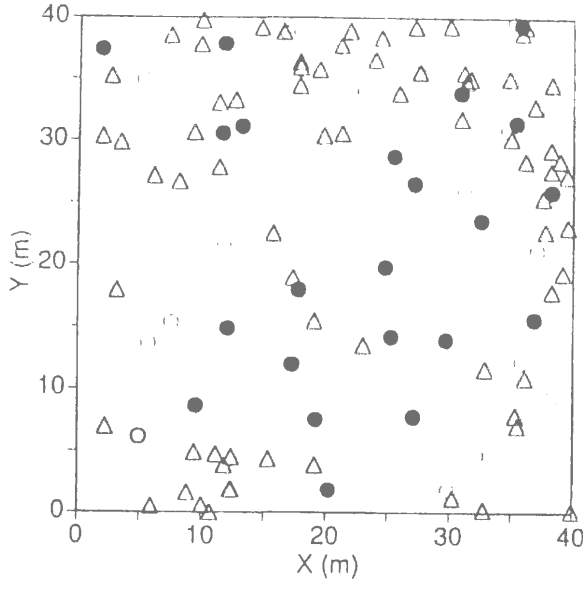

Fig. 2.10. Locations of large trees of *Podocarpus nagi* and *Neolitsea aciculata* in the 40 m × 40 m plot at Mt. Mikasa, Nara City, Japan. Solid circles, open circles and triangles represent large female trees of *P. nagi*, large male trees of *P. nagi* and large trees of *N. aciculata*, respectively.

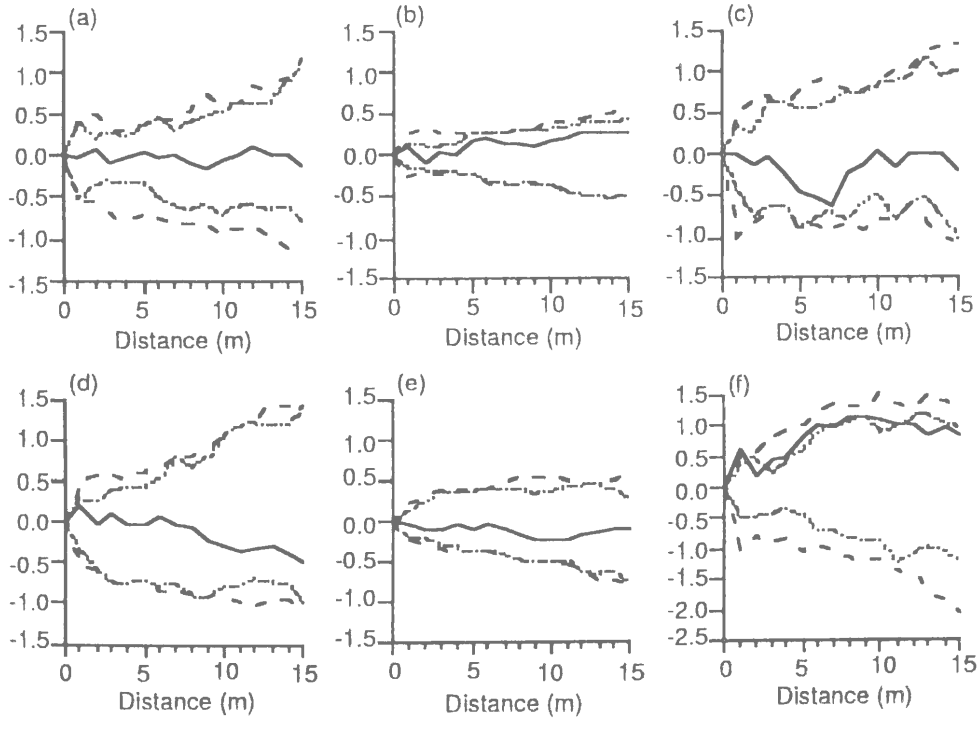

Fig. 2.11. $L_{12}(t)$ values of bivariate distribution of *Neolitsea aciculata* population and large trees of *Podocarpus nagi*: (a) 1-yr seedlings of *N. aciculata* and vs. large female trees of *P. nagi*, (b) saplings of *N. aciculata* vs. large female trees of *P. nagi*, (c) large trees of *N. aciculata* vs. large female trees of *P. nagi*, (d) 1-yr seedling of *N. aciculata* vs. large male trees of *P. nagi*, (e) saplings of *N. aciculata* vs. large male trees of *P. nagi*, (f) large trees of *N. aciculata* vs. large male trees of *P. nagi*. Conventions as in Fig. 2.6.

Discussion

The effects of seed dispersal ability and dioecy on the spatial pattern

The spatial pattern of plant species appears to be affected by the means of seed dispersion (Hubbell 1979; Briggs & Gibson 1992). The clumped distribution of small *Podocarpus nagi* plants could be explained in terms of small dispersal ability as often discussed (Prentice & Werger 1985; Sterner *et al.* 1986; Hatton 1989). Distribution of parent plants is also considered to affect the spatial heterogeneity of small plants. Spatial patterns of *P. nagi* shifted to a more regular distribution with increase of size (or age) as reported in many studies (Laessle 1965; Sterner *et al.* 1986; Kenkel 1988; Duncan 1991; Kenkel *et al.* 1997; Fulé & Covington 1998). This shift is expected to weaken the spatial heterogeneity of small plants. However, the density of small plants under half of the parent trees (male trees) of *P. nagi* was very low. Dioecy may create two phases with a different density of small plants in the area where *P. nagi* trees are dominant.

Among the various seed dispersal systems, bird dispersal is characterized by a wide distribution of seeds (Hubbell 1979; Murray 1988), and a high proportion of seeds is removed from the vicinity of the parent plants (Holthuijzen *et al.* 1987). For *Neolitsea aciculata*, the range of seed dispersal has been suggested to be so broad that the spatial pattern of small plants did not depend on the location of the female trees. Wide seed dispersal of *N. aciculata* weakened the effect of dioecy on the spatial heterogeneity of population structure.

Proposed three-phase dynamics model of coexistence

Briggs & Gibson (1992) observed a more clumped distribution with increasing tree height for three tree species and suggested that differential mortality of juveniles may promote clumping. Large *N. aciculata* trees showed distinct clumps and a significant attraction to large male *P. nagi* trees and a weak non-significant repulsive tendency with large female *P. nagi* trees. These results suggested that mortality and growth of *N. aciculata* were different under large male and female *P. nagi* trees and the environment around large male *P. nagi* trees might be the regeneration niche (Grubb 1977) for *N. aciculata*.

We propose a tentative three-phase dynamics model for explaining the mechanisms underlying the spatial patterns and examine the probability of coexistence of

the two species (Fig. 2.12). The model is based on the following assumptions: (1) *P. nagi* is more shade tolerant than *N. aciculata*; (2) *P. nagi* has limited seed dispersal around large female trees; and (3) *N. aciculata* has sufficient seed dispersal ability to occur arbitrary throughout the forest.

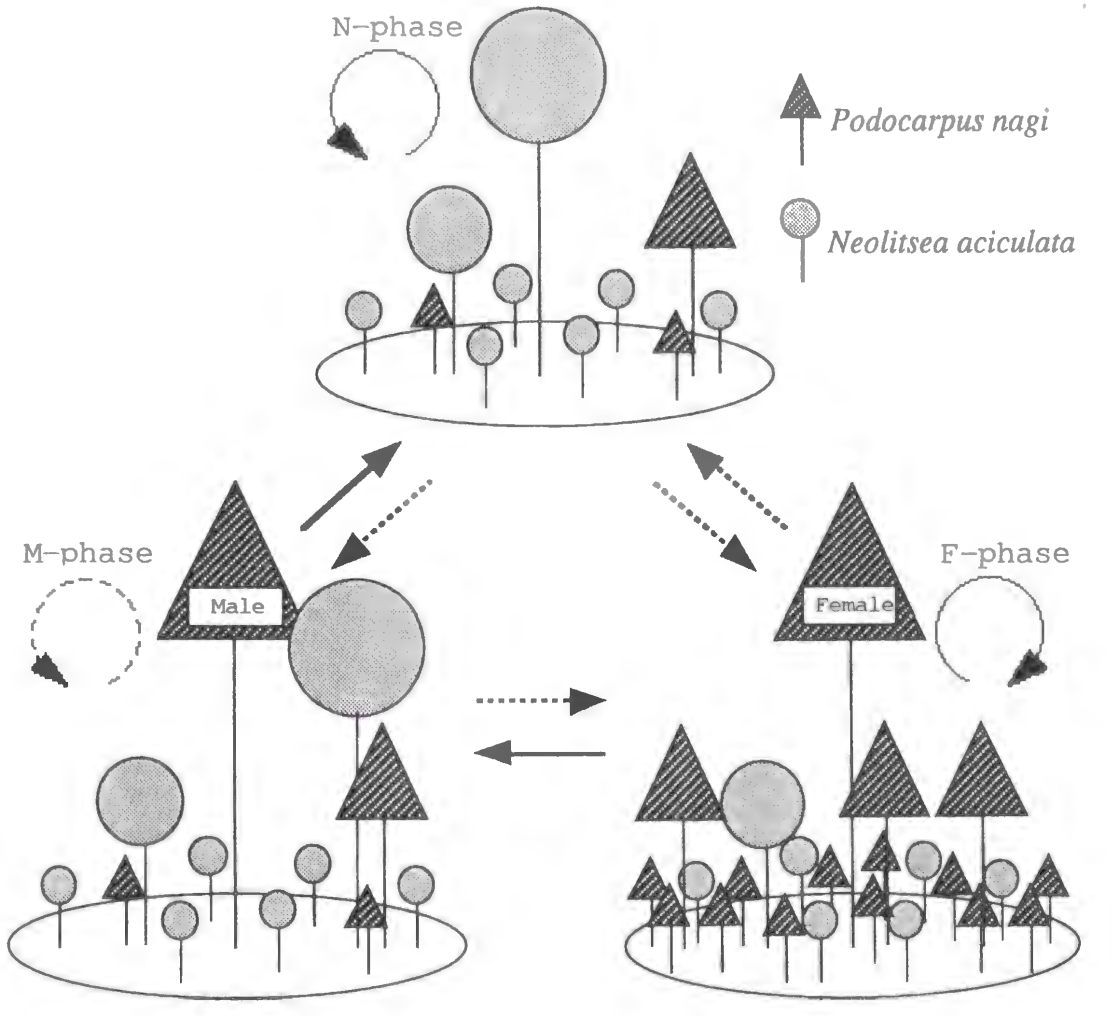

Fig. 2.12. Schematic diagram of regeneration patterns in *Podocarpus nagi* and *Neolitsea aciculata* suggested by spatial analyses. Direction of replacement in canopy trees is shown by arrows. The solid lines with arrow heads indicate transitions that occur frequently, and the broken line with arrow heads indicate transitions that occur occasionally.

Forest stands were divided into three phases based on the canopy trees: M-phase, where male *P. nagi* dominated the canopy; F-phase, where female *P. nagi* dominated the canopy; and N-phase, where *N. aciculata* or other species dominated the canopy. The

density of young *P. nagi* plants is higher at the F-phase and lower at the M phase. At the F-phase, canopy trees are regenerated by *P. nagi* with a high probability, because of the high density of successive young *P. nagi* plants. If the regenerated tree is female *P. nagi*, the F-phase is replaced by the F-phase, and if the regenerated tree is male *P. nagi*, the F-phase is replaced by the M-phase. At the M-phase, *N. aciculata* can grow because the light level is sufficient due to the low density of competitive *P. nagi* plants. After male *P. nagi* trees die at the M-phase, the probability of replacement from the M-phase to the N-phase is higher than the probability of other replacements. Even if *P. nagi* once occupied a given area, the area becomes the M-phase with 50% probability and will be replaced by other species. On the other hand, seedlings of *N. aciculata* occur arbitrarily throughout the three phases.

The model suggested that coexistence of *N. aciculata* with *P. nagi* could be facilitated by the environment under large male *P. nagi* trees, in which understory competition for light was considered to be much less intense for *N. aciculata*. In the area occupied by *P. nagi*, male *P. nagi* trees, which accounted for 50% of reproductive trees, were expected to create inevitably the environment in which density of young *P. nagi* plants was low. This appeared to be the dioecy effect on spatial structure of *P. nagi* population. The creation of the regeneration niche (Grubb 1977) for *N. aciculata* might be caused by the wide seed dispersal range of *N. aciculata* and the population structure of *P. nagi* itself. Our model was based on the location of trees at one time and they should be tested by further information on forest dynamics, i.e., measurements on the germination, growth, survival and mortality.

Chapter 3

Sex ratio and gender-dependent neighbouring effects in *Podocarpus nagi*, a dioecious tree species

Introduction

In dioecious plants, life history traits are often sex-related. Males, in comparison with females, showed smaller mature size or younger mature age (Clark & Clark 1987; Thomas & LaFrankie 1993), greater vegetative growth rate (Lloyd & Webb 1977; Hoffmann & Allende 1984; Obeso 1997), higher survival rate (Lloyd & Webb 1977; Lovett Doust & Lovett Doust 1988; Allen & Antos 1993) and superior competitive ability (Onyekwelu & Harper 1979; Cox 1981; Herrera 1988; Allende & Harper 1989). These intersexual differences were often explained by a higher reproductive cost in females than in males.

The gender-dependent life history traits induced sex-related population structures. Sex ratios were often male-biased (Opler & Bawa 1978; Waser 1984; Clark & Clark 1987; Lovett Doust & Lovett Doust 1988; Vasiliauskas & Aarssen 1992; Thomas & LaFrankie 1993; Gibson & Menges 1994; Nicotra 1998), though a female bias also was observed (Opler & Bawa 1978; Dawson & Bliss 1989; Allende & Harper 1989). Different size structure was observed between sexes because males were often over-represented in particular size classes (Opler & Bawa 1978; Ackerly *et al.* 1990; Thomas & LaFrankie 1993). Spatial variation in resource availability caused spatial segregation of males and females. Males were more common in a harsher environment, such as xeric and poor nutrient sites (Freeman *et al.* 1976; Grant & Mitton 1979; Bierzychudek & Eckhart 1988; Dawson & Bliss 1989; Iglesias & Bell 1989). In the local scale, analyses in plant to plant distances suggested that intersexual differences in resource requirement and competitive ability might cause spatial patterns in males and females (Herrera 1988; Allende & Harper 1989).

Sex ratio and sex-related spatial structures could affect population dynamics of dioecious species. The sex ratio of a population influences on the amount of total seed production (Mack 1997; Van Uden *et al.* 1998). The location of seed sources and their seed dispersal ability determined the initial spatial pattern of offspring (Augspurger 1983;

Houle 1992) and eventual spatial structure of populations (Hubbell 1979, Sterner *et al* 1989; Armesto *et al.* 1991). In Chapter 2, the spatial patterns of two codominant dioecious tree species, *Podocarpus nagi* (Thunb.) Zoll. et Moritz. (Podocarpaceae) and *Neolitsea aciculata* (Blume) Koidz. (Lauraceae) were analysed. *Podocarpus nagi* has a higher shade tolerance but narrower seed dispersal range than *N. aciculata*. They suggested that the dioecy-induced spatial heterogeneity of plant density in the *P. nagi* population might facilitate the growth of *N. aciculata* under male *P. nagi* trees where young *P. nagi* trees were uncommon.

The abundance and location of seed sources, i.e. sex ratio and sex-related spatial structure of *P. nagi* could be crucial factors for regeneration of *P. nagi* and *N. aciculata*. We aimed to evaluate the driving force of sex-related population structures of *P. nagi* and to discuss the effects of sex-related population structures of *P. nagi* on the community dynamics of *P. nagi* and *N. aciculata*. We analysed sex-related population structure and life history traits of *P. nagi* at various size classes: (1) sex ratio of reproductive trees; (2) growth rates of males and females; (3) spatial patterns of males and females; 4) the intensity of competition within sexes and between sexes. For long-lived plants, investigations accounting for sex and size/age interactions are useful to understand the processes in developing sex-related population structures (Alliende & Harper 1989; Vasiliauskas & Aarssen 1992; Allen & Antos 1993; Gibson & Menges 1994; Nicotra 1998).

Methods

Field methods

In 1988, a 1.48 ha plot (40 m × 370 m) was established from the foot to the peak of Mt. Mikasa (Chapter 2). The plot was divided into 5 m × 5 m quadrats. Within each quadrat, the x and y coordinates of the centre of all plants larger than 5 cm in stem diameter at breast height (d.b.h., 130 cm above ground level) were mapped, and their species and size were recorded. The total numbers of *P. nagi*, *N. aciculata* and other species within the plot were 1217, 1546 and 264 in 1992, respectively. For each plant of *P. nagi* within the whole plot larger than 5 cm in d.b.h., sex was determined by observing reproductive organs through binoculars. Strobili were observed for each tree in 1989, 1991, 1993 and 1995 because *P. nagi* reproduced every two years (S. Nanami, H. Kawaguchi & T.

Yamakura, unpublished data).

In March 1992, aluminum band type dendrometer (Hall 1944; Liming 1957) was installed on each tree at breast height (130 cm above ground level). This instrument consists of a band of aluminum for encircling the tree trunk in place by a coil spring. When the plot was resampled annually, tree status (living or dead) was recorded and diameter growth of a trunk was measured by the slide length of aluminum band from 1992 to 1998.

Data analysis

We carried out data analyses in the lower 40 m × 280 m part of the plot, because in the upper 40 m × 90 m part of the plot *P. nagi* had scarcely invaded yet and the density of *P. nagi* is lower than in the whole plot (81 ha $^{-1}$ vs. 822 ha $^{-1}$). The population of *P. nagi* was divided into groups depending on sex (male, female and unsexed) and size (d.b.h. classes) for the following analyses.

Deviation of sex ratio from 1:1 was tested by chi-square test on the whole population and on several size classes.

To detect gender-dependent spatial structures and effects of local competition on growth, a simple dichotomy of size classes, 5 ≤ d.b.h. < 30 cm and d.b.h. ≥ 30 cm in 1992, was employed for sexed *P. nagi* trees (Chapter 2). All trees with d.b.h. ≥ 30 cm reproduced except one tree with a d.b.h. of 30.0 cm.

Spatial patterns of trees within sexes or sizes were analysed using Ripley's $K(t)$ function (Ripley 1977; Diggle 1983; Upton & Fingleton 1985). The $K(t)$ function uses all tree-tree distances to provide a measure of spatial pattern at various distances t.

A square-root transformation of $K(t)$ suggested by Besag (1977) is easier to use:

$$L(t) = [K(t)/\pi]^{1/2} - t \qquad (1)$$

A value of $L(t) = 0$ indicates that the spatial pattern at distance t is random. Values of $L(t) > 0$ indicate clumped distributions, whilst values of $L(t) < 0$ indicate regular distributions.

Spatial interactions between two groups of trees were analysed using the bivariate function $L_{12}(t)$, a transformation of function $K_{12}(t)$ (Lotwick & Silverman 1982):

$$L_{12}(t) = [K_{12}(t)/\pi]^{1/2} - t \qquad (2)$$

A value of $L_{12}(t) = 0$ indicates that the two groups are spatially independent, values of $L_{12}(t) > 0$ indicate a positive association (attraction) and values of $L_{12}(t) < 0$ indicate a negative association (repulsion).

Significance of deviations from the null hypothesis was determined with Monte Carlo simulations (Besag 1977; Besag & Diggle 1977; Marriott 1979). The null hypothesis is complete spatial randomness for analysis of the univariate spatial pattern of trees, and spatial independence for analysis of bivariate spatial interactions between two groups. Ninety-five per cent confidence envelopes were defined as the highest and lowest values of $L(t)$ or $L_{12}(t)$ for each spatial scale found in 19 analyses of random point distributions. Ninety-nine per cent confidence envelopes require 99 simulations. See earlier uses of $L(t)$, $L_{12}(t)$ and Monte Carlo simulations (e.g. Kenkel 1988; Duncan 1991; Peterson & Squiers 1995; Haase 1995; Chapter 2).

To investigate intra- and intersexual effects of local competition on the growth of *P. nagi*, partial correlation coefficients were calculated between absolute growth rate of stem diameter (*AGR*) and local crowding of neighbouring trees. Tree size was also taken into account for partial correlation analyses, because size dependence of growth rate was often observed (Duncan 1991; Nakashizuka & Kohyama 1995; Hara *et al.* 1995; Kubota & Hara 1995). Partial correlation coefficient measures the correlation between any pair of variables when other variables are held constant (Sokal & Rohlf 1995). For calculating indices of local crowding for each target tree, sum of basal area at breast height of "neighbours" were used. This index has been used in Weiner (1984), Nakashizuka & Kohyama (1995) and Kubota & Hara (1995). In our study, trees within 5 m from target trees were used as "neighbours" (Duncan 1991; Stoll *et al.* 1994). Indices of local crowding were calculated for four categories of neighbours, i.e. male *P. nagi*, female *P. nagi*, unsexed *P. nagi* and other species. Trees within a 30 m × 270 m part inside of the 40 m × 280 m plot were used as target trees, because trees close to the plot edges had neighbours outside the plot that were not measured.

Results

Size distribution

Of 1188 *Podocarpus nagi* trees larger than 5 cm in d.b.h. in 1992 in the 40 m × 280 m

plot, 21 trees died by 1998. Of 1167 trees living in 1998, males, females and unsexed trees accounted for 373 (32%), 213 (18%) and 581 (50%), respectively. The shapes of size distribution were different among unsexed, male and female trees (Fig. 3.1).

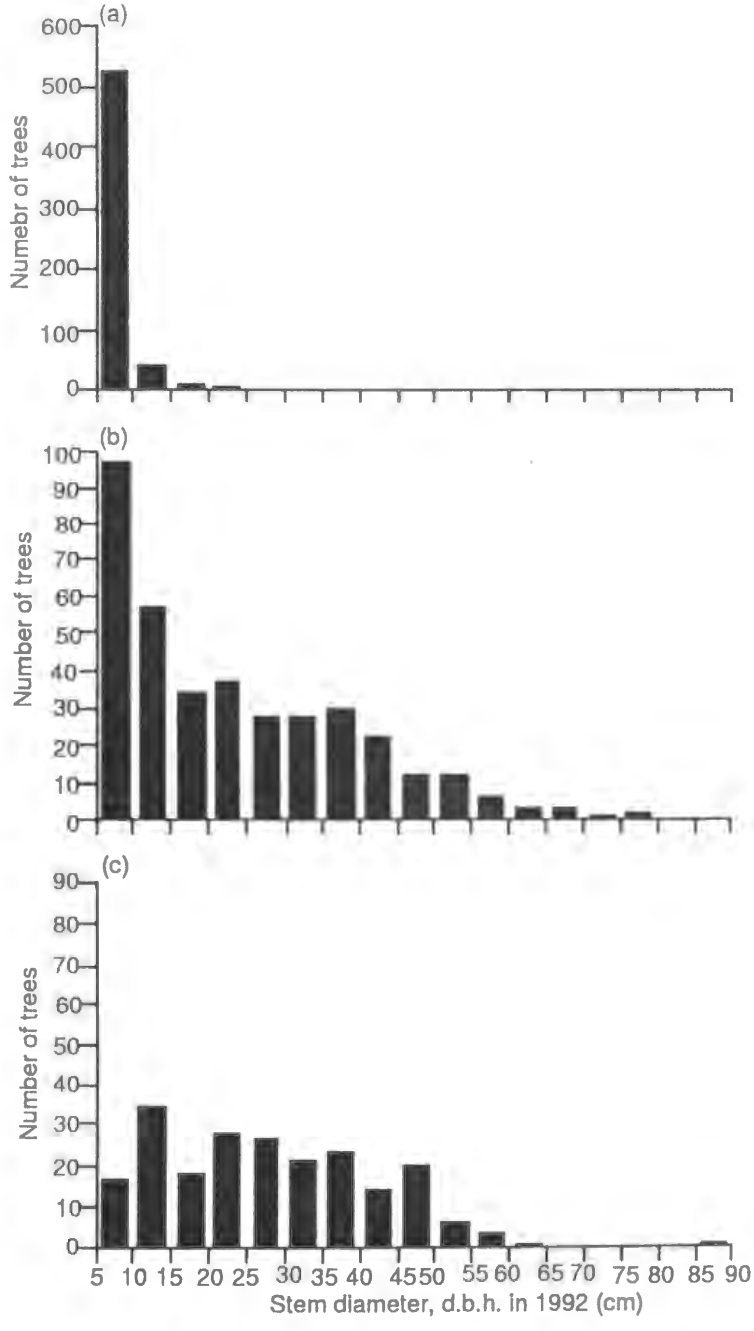

Fig. 3.1. Frequency distributions of d.b.h. (stem diameter at 130 cm height) in 1992 for (a) unsexed ($n = 581$), (b) male ($n = 373$) and (c) female ($n = 213$) *Podocarpus nagi* trees in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan.

Most of the unsexed trees were smaller than 10 cm d.b.h. The number of unsexed trees tended to decrease with increasing tree size and all trees larger than 30.0 cm in d.b.h. were sexed. Male trees showed a L-shaped distribution with a higher skewness and female trees with a lower skewness.

The sex ratio of reproductive trees larger than 5 cm in d.b.h. were significantly male- biased (male/female ratio of 1.75, $\chi^2 = 43.7$, $P < 0.001$) (Fig. 3.2). Males were predominant in all size classes, and sex ratio were significantly male-biased in $5 \leq$ d.b.h. < 20 cm class (male/female ratio of 2.72, $\chi^2 = 55.1$, $P < 0.001$) and in ≥ 50 cm d.b.h. class (male/female ratio of 2.55, $\chi^2 = 7.41$, $P < 0.01$). Sex ratio did not depart from 1:1 in $20 \leq$ d.b.h. < 50 cm classes.

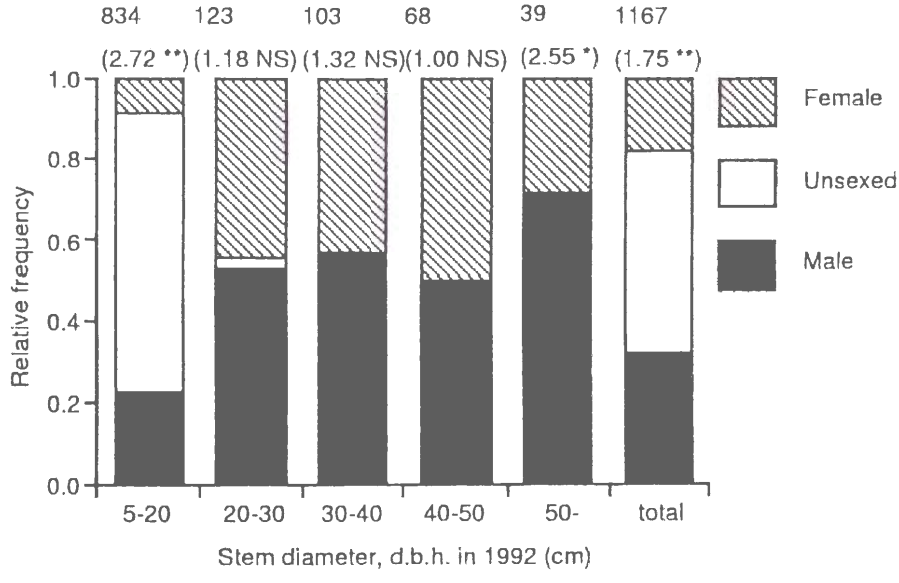

Fig. 3.2. Relative frequency of unsexed, male and female *Podocarpus nagi* trees in each d.b.h. (stem diameter at 130 cm height) class in 1992 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan. Sample size is indicated above each bar. The values in parentheses are male/female ratios and significance of deviation from the expected of 1:1 sex ratios (χ^2 test); $*P < 0.01$, $**P < 0.001$, NS. $P \geq 0.05$.

Growth rate

The growth rate of stem diameter had large variations within sexes and size classes (Fig 3.3). For male trees, median growth rate significantly differed among size classes ($P <$ 0.0001). The median growth rate was smaller in the smallest size class ($5 \leq$ d.b.h. < 20

cm) than in larger classes (d.b.h. ≥ 20 cm). For female trees, significant dependence of growth rate on tree size was not observed.

Females had a higher median growth rate than males in the smallest size class (5 ≤ d.b.h. < 20 cm) (marginally significant, $P = 0.051$, Mann-Whitney test,) and median growth rates did not significantly differ between sexes in other classes (Fig. 3.3). In d.b.h. ≥ 20 cm classes, however, 75th and 90th percentiles of growth rates of males were larger than those of females, suggesting the proposed male-biased sex ratio of trees with high growth rates.

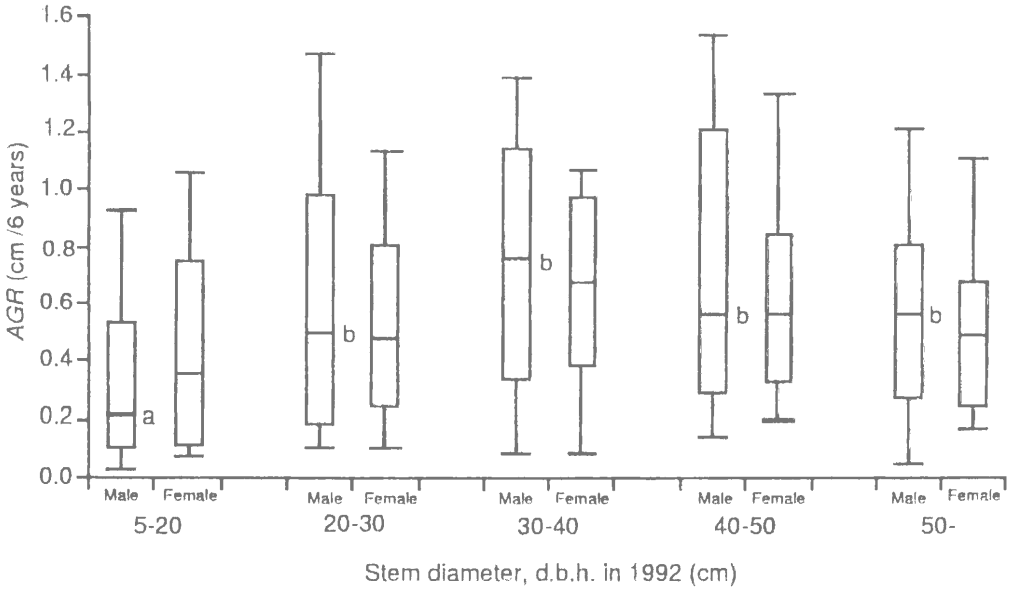

Fig. 3.3. Boxplot of absolute growth rates (*AGR*, cm/6 years) of stem diameter of male and female *Podocarpus nagi* in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan. Lower, middle and upper lines of each box represent 25th, 50th and 75th percentiles, respectively. The lower and upper whiskers represent 10th and 90th percentiles, respectively. Median of growth rates of male trees are significantly different among size classes ($P < 0.0001$, Kruskal-Wallis test). Values denoted by the same letters are not significantly different from each other at $P < 0.05$ (Mann-Whitney test). For female trees, median of growth rates are not significantly different among size classes ($P = 0.07$, Kruskal-Wallis test).

Thus, we divided the population into four groups based on growth rate (lower and higher than 1.0 cm/6 years) and d.b.h. (smaller and larger than 20 cm) and compared sex ratio among groups (Table 3.1). The sex ratio of trees with high growth rates was significantly male-biased in d.b.h. ≥ 20 cm groups.

Table 3.1. The differences of sex ratio between *Podocarpus nagi* trees with low and high absolute growth rates (*AGR*, cm/6 years) of stem diameter were tested by chi-square test in two size classes. Four males and four females were excluded from test because growth rates were not determined due to breakdown of dendrometers

	5 ≤ d.b.h. < 20 cm in 1992			D.b.h. > 20 cm in 1992		
	Number of	Number of	Male/Female	Number of	Number of	Male/Female
$0 < AGR < 1.0$	168	59	2.85	136	119	1.14
$AGR \geq 1.0$	18	8	2.25	47	23	2.04
			NS			$P < 0.05$

Spatial distribution

Analysis of the spatial distribution of *P. nagi* trees (Fig. 3.4) showed that small male trees (5 ≤ d.b.h. < 30 cm) were significantly ($P < 0.01$) clumped at all distances between 1 and 15 m (Fig. 3.5a). Small female trees were significantly clumped at 4 m ($P < 0.05$), 6–15 m ($P < 0.01$) (Fig. 3.5c). Large male trees (≥ 30 cm d.b.h.) were significantly clumped at 6–8 m ($P < 0.05$), 9–14 m ($P < 0.01$) and 15 m ($P < 0.05$) (Fig. 3.5b). Large female trees showed a random distribution except at 13 m (Fig. 3.5d).

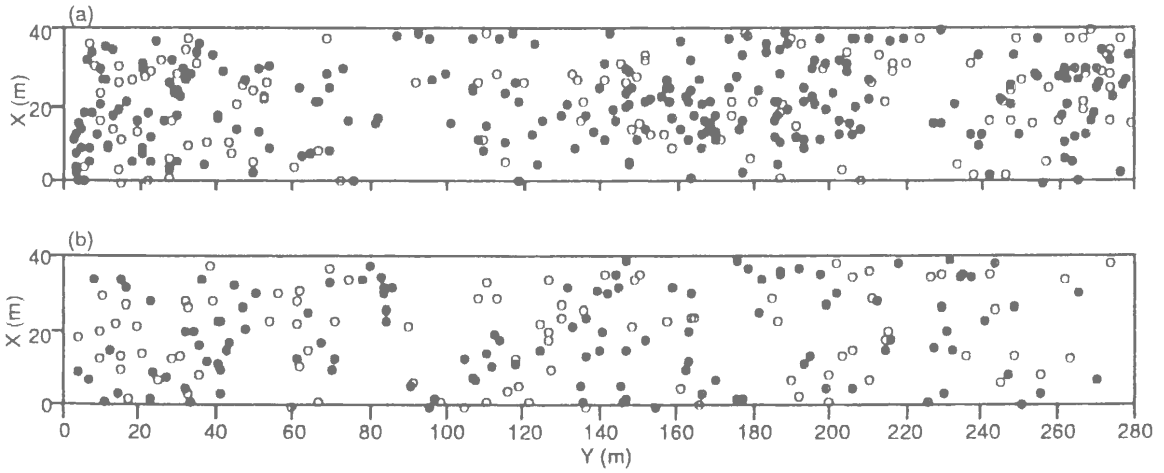

Fig. 3.4. The spatial distribution of male and female *Podocarpus nagi* trees in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) small trees (5 ≤ d.b.h. < 30 cm, n = 377) and (b) large trees (d.b.h. ≥ 30 cm, n = 209). Solid and open circles show male and female trees, respectively.

Small male and female trees showed a significant attraction at 1 m, 4–5 m, 8 m and 10–15 m ($P < 0.05$) (Fig. 3.6a). Large male and female trees showed a significant repulsion at 3 m ($P < 0.05$) and 4 m ($P < 0.01$) (Fig. 3.6b).

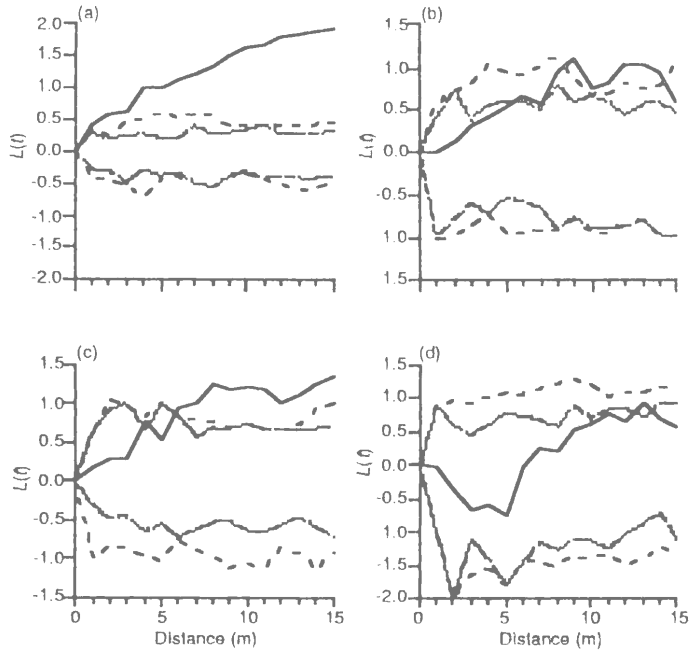

Fig. 3.5. $L(t)$ values for the *Podocarpus nagi* population in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) small male trees (n = 253); (b) large male trees (n = 120); (c) small female trees (n = 124); (d) large female trees (n = 89). The solid line shows actual $L(t)$ values for extant trees, dotted lines and broken lines show 95% and 99% confidence envelopes for the pattern expected from a random distribution of tree location, respectively. Values outside the envelopes indicate significant departure from randomness.

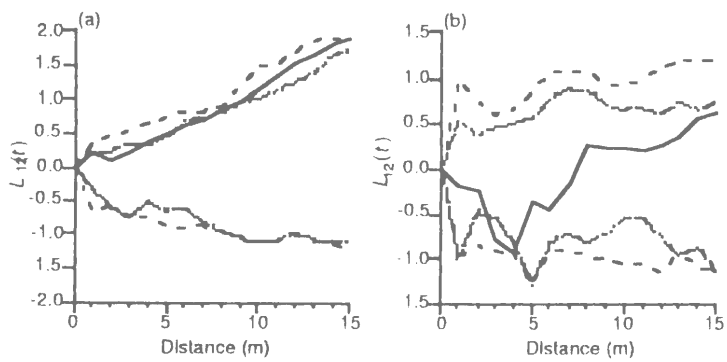

Fig. 3.6. $L_{12}(t)$ values of bivariate distribution of *Podocarpus nagi* population in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) small male trees vs. small female trees; (b) large male trees vs. large female trees. The solid line shows actual $L_{12}(t)$ values for extant trees, dotted lines and broken lines show 95% and 99% confidence envelopes for the pattern expected from an independent distribution of tree location, respectively. Values outside the envelopes indicate significant departure from independence.

Neighbouring effects on growth rate

The growth rate of small males ($5 \leq$ d.b.h. < 30 cm) was significantly dependent on their size ($P < 0.001$, Table 3.2). Effects of neighbouring trees on the growth rate of small males were not significant. The growth rate of small females showed a significantly negative partial correlation with local crowding of males ($P < 0.01$) and females ($P < 0.05$). Intrasexual and intersexual competition reduced the growth of females. Local crowding of unsexed *P. nagi* trees and other species did not have any significant neighbouring effects on the growth of either males or females. For large males and females (d.b.h. ≥ 30 cm), the growth rate did not show any significant partial correlation with tree size and local crowding of neighbouring trees.

Table 3.2. Partial correlations of absolute growth rate (*AGR*, cm/6 years) of stem diameter with tree size in d.b.h. and local crowding of male, female and unsexed *Podocarpus nagi* trees and the other species trees in a 30 m × 270 m subplot at Mt. Mikasa, Nara City, Japan. Local crowding was calculated as the sum of basal area at breast height of the neighbouring trees within 5 m from a target tree. *n* is the number of trees, *r* is the partial correlation coefficient, *P* is the probability of a Type I error for the null hypothesis. Three males and four females were excluded from test because growth rates were not determined due to breakdown of dendrometers

	5 ≤ d.b.h. < 30 cm in 1992				D.b.h. ≥ 30 cm in 1992			
	Males (n = 195)		Females (n = 92)		Males (n = 83)		Females (n = 62)	
	r	P	r	P	r	P	r	P
D.b.h. in 1992	0.400	< 0.001	0.078	0.469	0.043	0.706	−0.054	0.688
Local crowding of male *P. nagi*	−0.092	0.206	0.317	0.003	0.111	0.332	0.248	0.061
Local crowding of female *P. nagi*	−0.094	0.196	−0.257	0.016	0.143	0.210	0.069	0.605
Local crowding of unsexed *P. nagi*	0.003	0.972	0.173	0.108	0.053	0.645	0.073	0.589
Local crowding of other species	−0.035	0.633	0.065	0.547	−0.127	0.266	0.019	0.890

Discussion

Male-biased sex ratio and gender-dependent growth rate

Sex ratio according to size class was useful for the analysis of the sex-related population structure, because the onset of reproduction depends on the plant size (Clark & Clark 1987; Alliende & Harper 1989; Vasiliauskas & Aarssen 1992; Allen & Antos 1993; Thomas & LaFrankie 1993; Gibson & Menges 1994; Nicotra 1998). Unsexed trees of *P. nagi* decreased with increasing tree size, and the sex ratio in intermediate size classes ($20 \leq$ d.b.h. < 50 cm) did not depart from 1:1. These results suggested that the primary sex ratio of *P. nagi* can be considered to be unity (Nicotra 1998). The male-bias in the smallest size class ($5 \leq$ d.b.h. < 20 cm) was explained by the precocity of males relative to females. Among unsexed trees, unsexed females were considered to be over-represented. The growth rate of males became larger with increasing tree size (Table 3.2) and the median growth rate in the class of $5 \leq$ d.b.h. < 20 cm was smaller than that in d.b.h. ≥ 20 cm classes (Fig. 3.3), whereas in females the growth rate did not show size dependence. These results suggested that for the onset of reproduction, females require high resource availability as the large non-suppressed trees provided, while males could start to reproduce under low resource availability (Nicotra 1998). Differences in reproduction cost between sexes may determine the gender-dependent onset timing of reproduction.

Biased sex ratio in large size classes could be explained by differences in growth rate or mortality between sexes (Lloyd & Webb 1977; Allen & Antos 1993). If mortality is equal and growth rate is different between males and females in each size class, the sex ratio is expected to be biased, because a higher growth rate resulted in the shorter residence time at a given size class and the higher recruitment in the largest size class (Nicotra 1998). The number of males observed for trees with high growth rates larger than 20 cm in d.b.h. was significantly large (Table 3.1). This implies the female bias in the intermediate class and the male bias in the large size class. The sex ratio did not depart from the ratio 1:1 in the intermediate size classes ($20 \leq$ d.b.h. < 50 cm) , while the sex ratio was significantly male-biased in the large size class (d.b.h. ≥ 50 cm). This unexpected sex ratio in the intermediate size classes might be explained by the high mortality of females. The high mortality of females also could enhance the male bias in the large size class. The growth rate of individuals was often negatively correlated with mortality (Jenkins & Pallardy 1995; Pedersen 1998). Too few trees died during the study

period to examine the patterns of gender-dependent mortality. Significant male bias in the sex ratio of trees with high growth rates may indicate higher survival of male trees than of female trees.

Gender-dependent spatial pattern and neighbouring effects

The difference of competitive ability between sexes reported by previous studies (Cox 1981; Herrera 1988; Alliende & Harper 1989) could explain the gender-dependent patterns of *P. nagi*. In Chapter 2, it was reported that the small seed dispersal range of *P. nagi* caused the clump formation of young trees around large females. Young trees started to reproduce and small males and females occurred together in clumps (Figs 3.5 and 3.6). Large males and females shifted toward random distributions (Fig. 3.5b,d). Decrease in clumping intensity have often been reported to accompany an increase in tree size (or age) (Laessle 1965; Sterner *et al*. 1986; Kenkel 1988; Duncan 1991; Kenkel *et al.* 1997; Fulé & Covington 1998). Such a shift was more conspicuous for females than for males in *P. nagi* population, suggesting that repulsion occurred among females. Significantly negative intrasexual effect of neighbours on the growth of females (Table 3. 2) supported this suggestion. Intrasexual neighbouring effect on the growth of males was not significant (Table 3.2) and male clumps were preserved (Fig. 3.5a,b). The intrasexual negative effect of competition was detected among females but not among males. Intersexual effects of neighbours were significant on the growth of females but not on that of males (Table 3.2). Large males and females showed a significant repulsion at 3–4 m (Fig. 3.6b). This one-sided negative effect from males to females could cause the repulsion among males and females.

Both intrasexual and intersexual effects of neighbours were significant in females, though neither was significant in males. As a result, females would suffer from the presence of both males and females. Onyekwelu and Harper (1979) reported that the sex ratio of *Spinacia oleracea* did not deviate from 1:1 at a low plant density while it was male biased at a high plant density. If a large female of *P. nagi* occurs adjacent to large females, their seed rain overlap each other and the density of seedlings around the large female is expected to be larger than that around a large female adjacent to large males. In such a clump with a higher density of *P. nagi*, male dominancy may proceed.

The effects of sex-related population structure of Podocarpus nagi *on the community structure*

A male-biased sex ratio and non-random spatial patterns of males and females were observed in the *P. nagi* population. Since dioecy defines the crucial intersexual differences in seed dispersal ability, the seed-rain area in a forest is dependant on seed dispersal ability, abundance and locations of females. Seed dispersal of *P. nagi* was limited to the area around females due to low dispersal ability (Chapter 2). On the other hand, seed density became low in the area under males, where the area could be called a 'seed-rain gap'. In an area occupied by *P. nagi*, males will inevitably create seed-rain gaps. In Chapter 2, a three-phase dynamics model was proposed to explain the regeneration mechanisms of males and females of *P. nagi* and other species. The model suggested that the area under male *P. nagi* with a low density of young *P. nagi* might be the regeneration niche (Grubb 1977) for other species, especially for *N. aciculata* that has a large dispersal ability. In the model, the sex ratio of *P. nagi* was assumed to be 1:1. However, the observed sex ratio of large *P. nagi* was male-biased. A male-biased sex ratio implies less abundance of seed sources and more abundance seed-rain gap areas than in the case assuming that sex ratio is 1:1. A male-biased sex ratio of *P. nagi* may be favourable for regeneration success of other species.

Local combinations of males and females may also affect the seed-rain area. Females occurring close to males, compensate for the seed-rain gaps under males. However, if clumps of males not accompanied with females occur, the formation of seed-rain gaps becomes more accurate and they aggregate to be a large seed-rain gap. This tendency was supported by clumps of large males and repulsion between males and females (Figs 3.5 and 3.6). The revegetation of disturbance-created gaps is influenced by the size of the gap (Sousa 1984; Runkle 1985) and for species with a small dispersal ability, arrival to the gap centre and colonization of a gap are difficult if gap size is relatively larger than their dispersal ability (Sousa 1984; Schupp *et al*. 1989; Forget 1991; Kotanen 1997; Dalling *et al*. 1998). In the centre of male clumps, *P. nagi* may be difficult to colonize. A clumped distribution of male trees of *P. nagi* may be favourable for regeneration success of other species with large seed dispersal ability such as *N. aciculata*.

Chapter 4

Patch formation and coexistence of two tree species, *Podocarpus nagi* and *Neolitsea aciculata*

Introduction

In plant communities, competition occurs among neighbouring plants. Growth and mortality of individual plants are influenced by separation, local density, size and species composition of neighbours (Harper 1977; Mack & Harper 1977; Antonovics & Levin 1980; Weiner 1984). The competition among plants affects the species composition and population structure of each species in a plant community (Greig-Smith 1979; Fowler 1986). In monospecific stands, more regular spatial patterns have often been reported with an increase in plant size (or age) and such a shift has been explained to be induced by intraspecific competition (Laessle 1965; West 1984; Kenkel 1988; Kenkel *et al.* 1997). Similar shifts in spatial patterns have also been reported in multi-species stands (Christensen 1977; Phillips & MacMahon 1981; Sterner *et al.* 1986; Duncan 1991; Fulé & Covington 1998).

In multi-species stands, both intra- and interspecific competitions should be considered (Duncan 1991; Nakashizuka & Kohyama 1995 ; Hara *et al.* 1995; Kubota & Hara 1995, 1996; Peterson & Squiers 1995a,b). By interspecific competition, the habitat of species with inferior competitive ability was restricted to the sites where density of superior competitor was low (Gurevitch 1986; Haase *et al.* 1997; Bockelmann & Neuhaus 1999). Hart *et al.* (1989) reported that the superior competitive ability of species with large seeds and high shade tolerance resulted in the formation of monodominant stands within a species-rich tropical forest. Frelich *et al.* (1993) and Frelich *et al.* (1998) reported a mixed-species forest consisting of mono-specific patches and that interspecific competition was responsible for the patch formation.

The spatial structure of plants, on the other hand, affects competition (Duncan 1991; Hara *et al.* 1995; Kubota & Hara 1995, 1996). In multi-species stands, the spatial pattern of each species should be considered for studies on the competition, because the spatial pattern determine how often competing species encounter each other and therefore the intensity of intra- and interspecific competitions (Silvertown & Lovett Doust 1993).

The relative intensity of intra- and interspecific competitions could spatially fluctuate particularly in plant communities where partitioning of establishment sites occurred and population structures were clumped. The partitioning of establishment sites may permit the coexistence of tree species due to avoidance of interspecific competition (Duncan 1991; Kubota & Hara 1995) and may create spatial refuge of inferior competitors from superior competitors (Silvertown & Lovett Doust 1993). Competition and spatial pattern are interdependent, i.e., spatial patterns are formed by competition, and the intensity of competitive effects is affected by spatial patterns. However, the interactions between competition among plants and spatial patterns of plants have not been studied yet (but see Kubota & Hara 1995, 1996).

The present study describes the formation of spatial structure and competitive interactions among trees in a forest community dominated by two dioecious tree species, *Podocarpus nagi* (Thunb.) Zoll. et Moritz. (Podocarpaceae) and *Neolitsea aciculata* (Blume) Koidz. (Lauraceae) at Mt. Mikasa, Nara City, Japan. *Podocarpus nagi* has a higher shade tolerance but a narrower seed dispersal range than *N. aciculata*. In Chapter 2, it was reported that the narrow seed dispersal range and dioecy induced the spatial heterogeneity of plant density in the *P. nagi* population and suggested that the regeneration of *N. aciculata* was facilitated in the area where the density of *P. nagi* trees was low. However, their suggestion was based on the location of trees at one time and should be tested by gathering further information on forest dynamics, i.e., measurements of growth, survival and mortality of trees.

To infer the processes of pattern formation of the two species, we analysed the spatial structures of both species in various size classes, because the spatial pattern for each size (or age) class suggests the past process of regeneration (Sterner *et al.* 1989; Lusk & Ogden 1992). We analysed the changes in spatial patterns by tree mortality to detect any evidence of pattern formation, and the neighbouring effects on growth rate at various size classes to evaluate the relative importance of intra- and interspecific competition on pattern formation. Here, we discuss the coexistence mechanisms of *P. nagi* and *N. aciculata*.

Methods

Field methods

In 1988, a 1.48 ha plot (40 m × 370 m) was established on a northwest-facing slope (ca. 20° mean inclination) of Mt. Mikasa. The plot was divided into 5 m × 5 m quadrats. Within each quadrat, the x and y coordinates of all the trees larger than 5 cm in stem diameter at breast height (d.b.h., 130 cm above ground level) were mapped, and their species and d.b.h. were recorded. The total numbers of *P. nagi*, *N. aciculata* and other species within the plot were 1217, 1546 and 264 in 1992, respectively.

In March 1992, an aluminum band type dendrometer (Hall 1944; Liming 1957) was installed on each tree at breast height (130 cm above ground level). This instrument consists of a band of aluminum for encircling the tree trunk in place by a coil spring. When the plot was resampled annually, tree status (living or dead) was recorded and diameter growth of the trunk was measured by the slide length of the aluminum band from 1992 to 1998.

Data analysis

The purpose of this paper is to elucidate the coexistence mechanism of *P. nagi* (superior competitor) and *N. aciculata* (inferior competitor). Therefore, we analysed the data in the lower 40 m × 280 m part of the plot, because in the upper 40 m × 90 m part of the plot *P. nagi* had scarcely invaded yet and the density of *P. nagi* was lower than that in the whole plot (81 ha^{-1} vs. 822 ha^{-1}).

Spatial patterns

Spatial patterns of trees within a population were analysed using Ripley's $K(t)$ function (Ripley 1977). The function $\lambda K(t)$ (λ = intensity) is defined as the expected number of trees within distance t of an arbitrary tree. The unbiased estimate of $K(t)$ is defined as:

$$K(t) = n^{-2} |A| \sum_{i \neq j} \sum w_{ij}^{-1} I_t(u_{ij}),$$

where n is the number of trees in a plot A; $|A|$ denotes plot area; u_{ij} is the distance between ith tree and jth tree in A; $I_t(u)$ is equal to 1 if $u \leq t$ and 0 otherwise; w_{ij} is the

proportion of the circumference of a circle with centre at ith tree and radius u_{ij} that lies within A; and summation is for all pairs of trees not more than t apart (Ripley 1977; Diggle 1983; Upton & Fingleton 1985; Dale 1999). A square-root transformation of $K(t)$ suggested by Besag (1977) is easier to use: $L(t) = [K(t)/\pi]^{1/2} - t$. A value of $L(t) = 0$ indicates that the spatial pattern at distance t is random. Values of $L(t) > 0$ indicate clumped distributions, whilst values of $L(t) < 0$ indicate regular distributions. Since spatial patterns in each size class suggests the past process of regeneration (Stemer *et al.* 1989; Lusk & Ogden 1992), the life stage of each species was distinguished on the basis of tree size. The population of *P. nagi* was divided into four stages, i.e., $5 \leq$ d.b.h. < 10 cm, $10 \leq$ d.b.h. < 15 cm, $15 \leq$ d.b.h. < 30 cm and d.b.h. ≥ 30 cm. The population of *N. aciculata* was divided into three stages, i.e., $5 \leq$ d.b.h. < 10 cm, $10 \leq$ d.b.h. < 15 cm and d.b.h. ≥ 15 cm. Wider size intervals were used for *N. aciculata* than for *P. nagi* because *P. nagi* had a larger maximum d.b.h. than *N. aciculata* (see results).

Spatial interactions between *P. nagi* and *N. aciculata* trees were analysed using the bivariate function $L_{12}(t)$, a transformation of function $K_{12}(t)$ (Lotwick & Silverman 1982): $L_{12}(t) = [K_{12}(t)/\pi]^{1/2} - t$. The function $K_{12}(t)$ is a generalization of the function $K(t)$ to a bivariate point process. A value of $L_{12}(t) = 0$ indicates that the two species are spatially independent, values of $L_{12}(t) > 0$ indicate a positive association (attraction) and values of $L_{12}(t) < 0$ indicate a negative association (repulsion). In Chapter 2, it was reported that the regeneration of *N. aciculata* appeared to be facilitated where the density of *P. nagi* was low. To infer a competitive effect by *P. nagi* on the regeneration of *N. aciculata*, we analysed the competitive interaction of *N. aciculata* in three size classes with *P. nagi*. Assuming a one-sided competition, i.e., large trees suppress small trees but not vice versa (Weiner & Thomas 1986; Thomas & Weiner 1989; Kohyama 1991, 1992, 1993), *P. nagi* trees with smaller size than a given size class of *N. aciculata* were omitted. Thus, spatial interactions were analysed for *N. aciculata* in the $5 \leq$ d.b.h. < 10 cm class vs. *P. nagi* with d.b.h. ≥ 5 cm, *N. aciculata* in the $10 \leq$ d.b.h. < 15 cm class vs. *P. nagi* with d.b.h. ≥ 10 cm and *N. aciculata* with d.b.h. ≥ 15 cm vs. *P. nagi* with d.b.h. ≥ 15 cm.

The significance of both $L(t)$ and $L_{12}(t)$ functions was determined with Monte Carlo simulations (Besag 1977; Besag & Diggle 1977; Marriott 1979). For analysis of the univariate spatial pattern of trees, the null hypothesis is complete spatial randomness. For bivariate spatial interactions between two species, the null hypothesis is spatial independence. Ninety-nine per cent confidence envelopes were defined as the highest

and lowest values of $L(t)$ or $L_{12}(t)$ for each spatial scale found in 99 analyses of random point distributions. In this study, the 'intensity' of spatial patterns or spatial interactions is defined as the magnitude of the deviation from randomness (Rebertus *et al.* 1989). See earlier uses of $L(t)$, $L_{12}(t)$ and Monte Carlo simulations (e.g. West 1984, Kenkel 1988; Rebertus *et al.* 1989; Duncan 1991; Peterson & Squiers 1995b; Haase 1995).

Changes in spatial patterns

To test the change in the spatial pattern through time, we made simulations of random mortality from the initial *P. nagi* and *N. aciculata* populations in 1992. The locations of live trees in 1992 represent the pre-mortality spatial pattern. Random mortality was simulated by random selection and removal of trees from the pre-mortality data set. The number of removed trees corresponded to the number of dead trees from 1992 to 1998 and their removal represented one simulation of the random mortality process. The same method for analysing changes in spatial patterns was used in the previous studies (e.g. Kenkel 1988; Rebertus *et al.* 1989; Duncan 1991; Peterson & Squiers 1995b). Ninety-five per cent confidence envelopes were generated from high and low values of the function $L(t)$ calculated from 19 simulations of the random mortality process. Ninety-nine per cent confidence envelopes require 99 simulations. Values of the empirical function that lie outside these envelopes indicate patterns of non-random mortality. The mortality rate must be enough high to detect a spatial pattern change. Therefore, spatial pattern change was analysed for the $5 \leq$ d.b.h. < 7.5 cm class with the highest mortality rate (see results) in both *P. nagi* and *N. aciculata*.

Competitive effects on the growth of trees

To investigate the intra- and interspecific effects of local competition on the growth of trees, we calculated partial correlation coefficients between absolute growth rate of stem diameter for 6 years and local crowding of neighbouring trees. Tree size was also taken into account for partial correlation analyses, because size dependence of growth rate was often observed (Duncan 1991; Nakashizuka & Kohyama 1995; Hara *et al.* 1995; Kubota & Hara 1995). The partial correlation coefficient measures the correlation between any pair of variables when other variables are held constant (Sokal & Rohlf 1995). For calculating indices of local crowding around each target tree, the sum of the basal area at breast height of "neighbours" was used. This index has been used in the previous studies

(e.g. Weiner 1984; Nakashizuka & Kohyama 1995, Kubota & Hara 1995). In our study, trees within 5 m from target trees were used as "neighbours" (Duncan 1991; Stoll *et al.* 1994). Indices of local crowding were calculated for three tree categories, i.e., *P. nagi*, *N. aciculata* and other species. Assuming that competition was one-sided, neighbours smaller than a target tree were omitted for evaluation of local crowding. Trees within a 30 m × 270 m part inside of the 40 m × 280 m plot were used as target trees, because trees close to the plot edges had neighbours outside the plot that were not measured.

Results

Species composition

For plants that were larger than 5 cm d.b.h. in 1992, the 40 m × 280 m plot contained a total of 27 woody species. *Podocarpus nagi* and *N. aciculata* accounted for 48% and 47% respectively of the 2487 plants observed (Table 4.1). The vegetation was occupied mostly by *P. nagi* and *N. aciculata*, thus the two species were codominant at Mt. Mikasa. The remaining 25 species accounted for only 5%.

Table 4.1. Number of plants of woody species larger than 5 cm in d.b.h. in 1992 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan

Species	Number
Podocarpus nagi	1188
Neolitsea aciculata	1177
Other woody species	
Evergreen broad-leaved (7 spp.)	30
Deciduous broad-leaved (9 spp.)	27
Evergreen conifers (3 spp.)	5
Climbers (6 spp.)	60
Total	2487

Population structure of Podocarpus nagi *and* Neolitsea aciculata

Both *P. nagi* and *N. aciculata* showed a unimodal and inverse J-shaped d.b.h. distribution (Fig. 4.1), suggesting that recruitments of both species occurred continuously. Maximum d.b.h. of *P. nagi* and *N. aciculata* in 1992 were 88 cm and 37 cm, respectively.

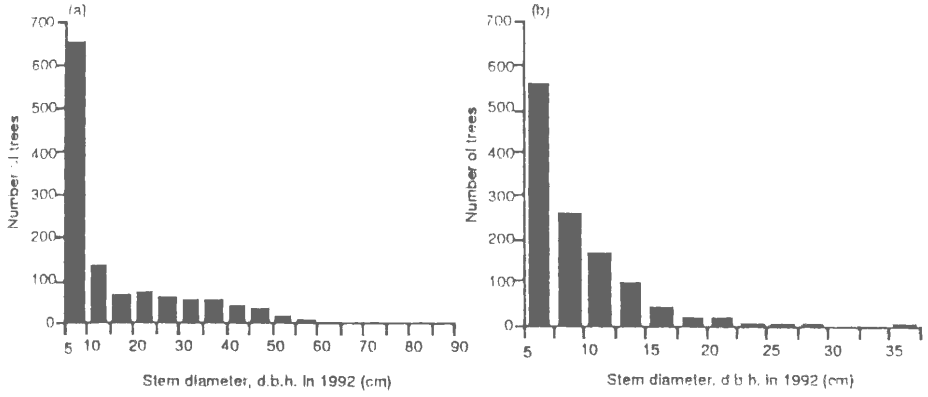

Fig. 4.1. Frequency distributions of d.b.h. (stem diameter at 130 cm height) in 1992 for (a) *Podocarpus nagi* (n = 1188) and (b) *Neolitsea aciculata* (n = 1177) in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan.

Analysis of the spatial pattern of *P. nagi* trees (Fig. 4.2a) showed that trees in the 5 ≤ d.b.h. < 10 cm class were significantly ($P < 0.01$) clumped at all distances between 1 and 15 m (Fig. 4.3a). *Podocarpus nagi* trees in the 10 ≤ d.b.h. < 15 cm class were significantly clumped at 3–15 m (Fig. 4.3b). *Podocarpus nagi* trees in the 15 ≤ d.b.h. < 30 cm class and with d.b.h. ≥ 30 cm showed a random distribution at 1–4 m and 1–7 m, respectively (Fig. 4.3c,d). The clumping intensity of *P. nagi* trees decreased progressively with increasing tree size.

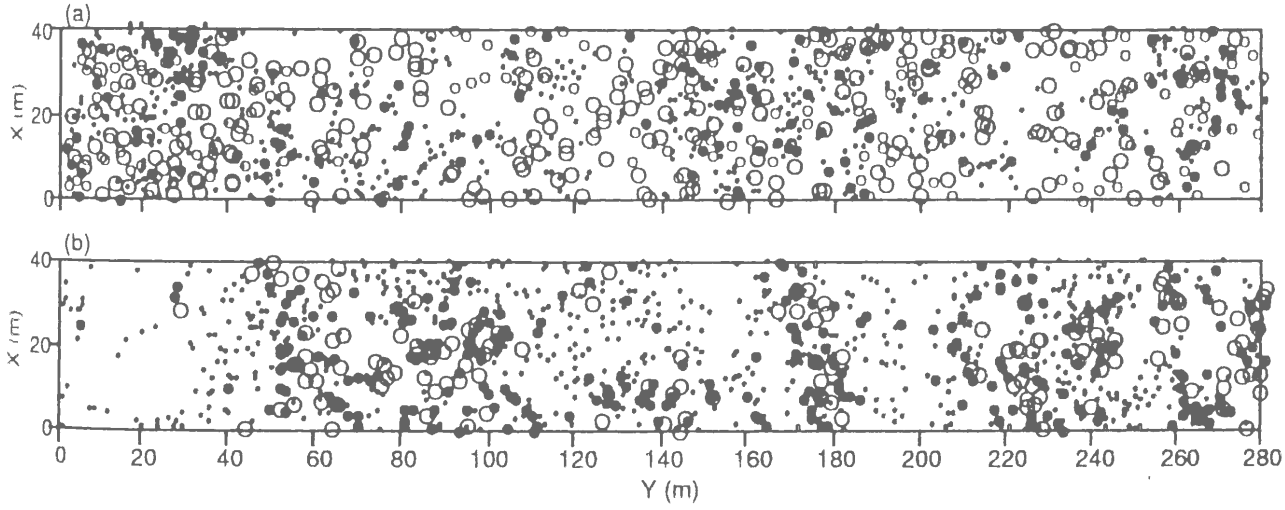

Fig. 4.2. The spatial distribution of the *Podocarpus nagi* population and the *Neolitsea aciculata* population in 1998 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) *Podocarpus nagi* trees. Small solid circles, large solid circles, small open circles and large open circles represent trees in the 5 ≤ d.b.h. < 10 cm (n = 621), 10 ≤ d.b.h. < 15 cm (n = 142), 15 ≤ d.b.h. < 30 cm (n = 184) and d.b.h. ≥ 30 cm (n = 220) classes, respectively. (b) *Neolitsea aciculata* trees. Small solid circles, large solid circles and open circles represent trees in the 5 ≤ d.b.h. < 10 cm (n = 710), 10 ≤ d.b.h. < 15 cm (n = 263) and d.b.h. ≥ 15 cm (n = 135) classes, respectively.

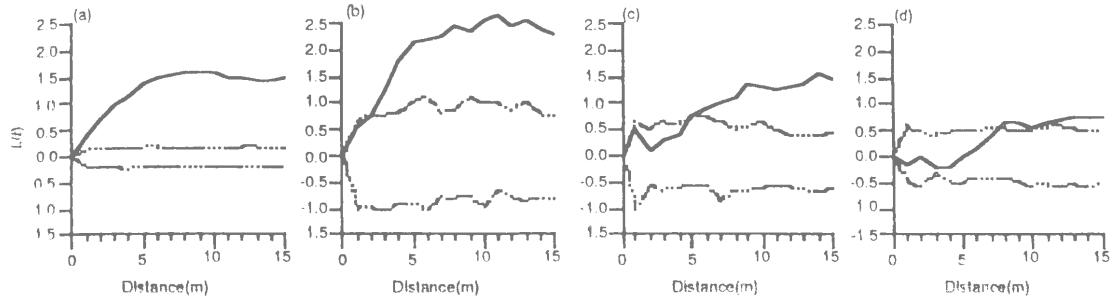

Fig. 4.3. $L(t)$ values for the *Podocarpus nagi* population in 1998 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) 5 ≤ d.b.h. < 10 cm, (b) 10 ≤ d.b.h. < 15 cm, (c) 15 ≤ d.b.h. < 30 cm, (d) d.b.h. ≥ 30 cm. The solid line shows actual $L(t)$ values for extant plants, dotted lines show 99% confidence envelopes for the pattern expected from a random distribution of tree locations. Values outside the envelopes indicate significant departure from randomness.

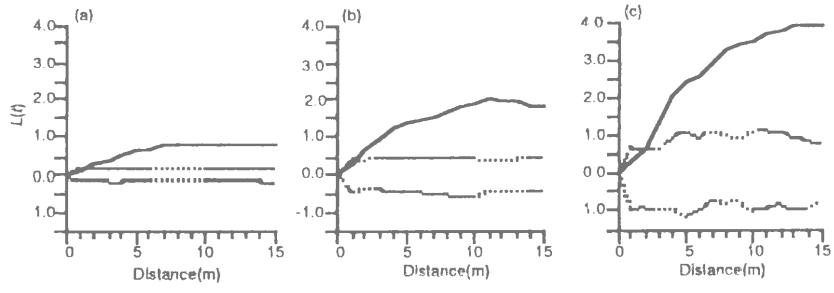

Fig. 4.4. $L(t)$ values of *Neolitsea aciculata* population in 1998 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) 5 ≤ d.b.h. < 10 cm, (b) 10 ≤ d.b.h. < 15 cm, (c) d.b.h. ≥ 30 cm. The solid line shows actual $L(t)$ values for extant plants, dotted lines show 99% confidence envelopes for the pattern expected from a random distribution of tree locations. Values outside the envelopes indicate significant departure from randomness.

Analysis of the spatial pattern of *N. aciculata* trees (Fig. 4.2b) showed that trees were significantly ($P < 0.01$) clumped at 2–15 m in all three size classes (Fig. 4.4a,b,c). For *N. aciculata* trees, the clumping intensity increased progressively with increasing tree size.

Neolitsea aciculata trees in the 5 ≤ d.b.h. < 10 cm class showed a significant ($P < 0.01$) repulsion from *P. nagi* trees with d.b.h. ≥ 5 cm at 3–15 m (Fig. 4.5a). *Neolitsea aciculata* trees in the 10 ≤ d.b.h. < 15 cm class showed a significant ($P < 0.01$) repulsion from *P. nagi* trees with d.b.h. ≥ 10 cm at 2–15 m (Fig. 4.5b). *Neolitsea aciculata* trees with d.b.h. ≥ 15 cm showed a significant ($P < 0.01$) repulsion from *P. nagi* trees with d.b.h. ≥ 15 cm at 2–15 m (Fig. 4.5c). The degree of repulsion of *N. aciculata* from *P. nagi* increased progressively with increasing tree size.

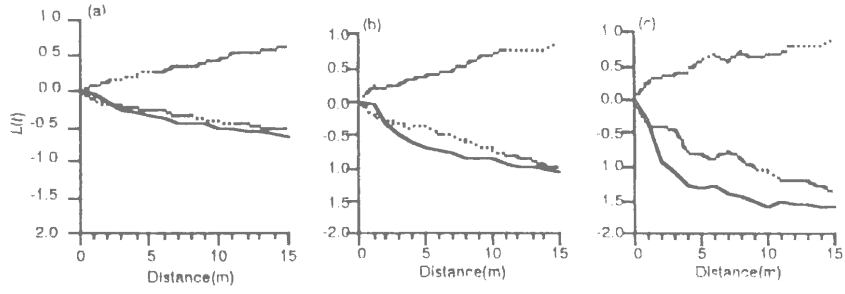

Fig. 4.5. $L_{12}(t)$ values of bivariate distribution of *Neolitsea aciculata* population and *Podocarpus nagi* population in 1998 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan: (a) *N. aciculata* trees with 5 ≤ d.b.h. < 10 cm vs. *P. nagi* trees with d.b.h. ≥ 5 cm, (b) *N. aciculata* trees with 10 ≤ d.b.h. < 15 cm vs. *P. nagi* trees with d.b.h. ≥ 10 cm, (c) *N. aciculata* trees with d.b.h. ≥ 15 cm vs. *P. nagi* trees with d.b.h. ≥ 15 cm. The solid line shows actual $L_{12}(t)$ values for extant plants, dotted lines show 99% confidence envelopes for the pattern expected from an independent distribution of tree locations, respectively.

Changes in spatial patterns due to mortality

The mortality of trees varied among species and size classes (Fig. 4.6). The mortality rate of *N. aciculata* was significantly higher than that of *P. nagi* in the 5 ≤ d.b.h. < 7.5 cm ($P < 0.0001$) and 7.5 ≤ d.b.h. < 10 cm classes ($P < 0.05$) (Fisher's exact probability test). Mortality rates of both species were highest in the smallest size class, 5 ≤ d.b.h. < 7.5 cm class, and decreased with increasing size class but increased slightly in the d.b.h. ≥ 15 cm class.

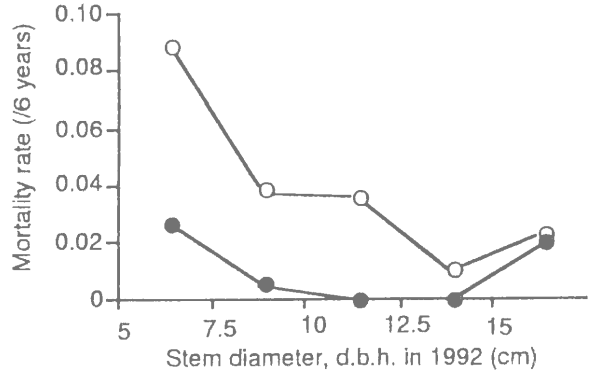

Fig. 4.6. Relationship between d.b.h. (stem diameter at breast height, 130 cm) in 1992 and mortality rate from 1992 to 1998 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan. Solid and open circles represent the rates in each d.b.h. class of *Podocarpus nagi* and *Neolitsea aciculata*, respectively.

The change in spatial patterns due to mortality was analysed for each species in the 5 ≤ d.b.h. < 7.5 cm class (Table 4.2). For *N. aciculata*, the initial number of trees in the 5 ≤ d.b.h. < 7.5 cm class in 1992 was 561. Fifty *N. aciculata* trees had died by 1998. The number of living trees was 511 in 1998. The living trees in 1998 were significantly more clumped at 6 m ($P < 0.01$), 7–8 m ($P < 0.05$), 9 m ($P < 0.01$), 10–11 m ($P < 0.05$) and 12 m ($P < 0.01$) than the expected distribution where mortality of trees was simulated to be randomly chosen from the initial spatial distribution. For *P. nagi* trees, the mortality rate for 6 years was low (12/456 = 0.026) and no significant change in spatial pattern was detected (Table 4.2).

Table 4.2. Changes in $L(t)$ values of trees with 5 ≤ d.b.h. < 7.5 cm of *Podocarpus nagi* and *Neolitsea aciculata* in the 40 m × 280 m subplot at Mt. Mikasa, Nara City, Japan. $*P < 0.05$, $**P < 0.01$

	$L(t)$ for *Podocarpus nagi*			$L(t)$ for *Neolitsea aciculata*		
Distance (m)	Live in 1992 (n = 456)	Live in 1998 (n = 444)	Change of $L(t)$	Live in 1992 (n = 561)	Live in 1998 (n = 511)	Change of $L(t)$
1	0.396	0.382	−0.014	−0.001	0.046	+0.047
2	0.778	0.769	−0.009	0.217	0.275	+0.058
3	0.967	0.965	0.002	0.391	0.426	+0.035
4	1.173	1.179	0.006	0.497	0.567	+0.070
5	1.344	1.352	0.008	0.587	0.670	+0.083
6	1.449	1.455	0.006	0.617	0.729	+0.112 **
7	1.459	1.459	0.000	0.724	0.860	+0.136 *
8	1.428	1.430	0.002	0.754	0.877	+0.123 *
9	1.380	1.373	0.007	0.782	0.934	+0.152 **
10	1.358	1.359	0.001	0.762	0.875	+0.113 *
11	1.303	1.302	−0.001	0.743	0.870	+0.127 *
12	1.259	1.275	0.016	0.752	0.885	+0.133 **
13	1.231	1.250	0.019	0.701	0.820	+0.119
14	1.240	1.269	0.029	0.741	0.865	+0.124
15	1.287	1.322	0.035	0.676	0.817	+0.141

Neighbouring effects of crowding on growth rate

The absolute growth rate of stem diameter for 6 years varied among species and size classes (Fig. 4.7). The growth rate of *P. nagi* and *N. aciculata* showed size dependency. The growth rate tended to be larger with increasing tree size. In all size classes, the growth rate of *N. aciculata* was significantly ($P < 0.05$) larger than that of *P. nagi* (Mann-Whitney test)

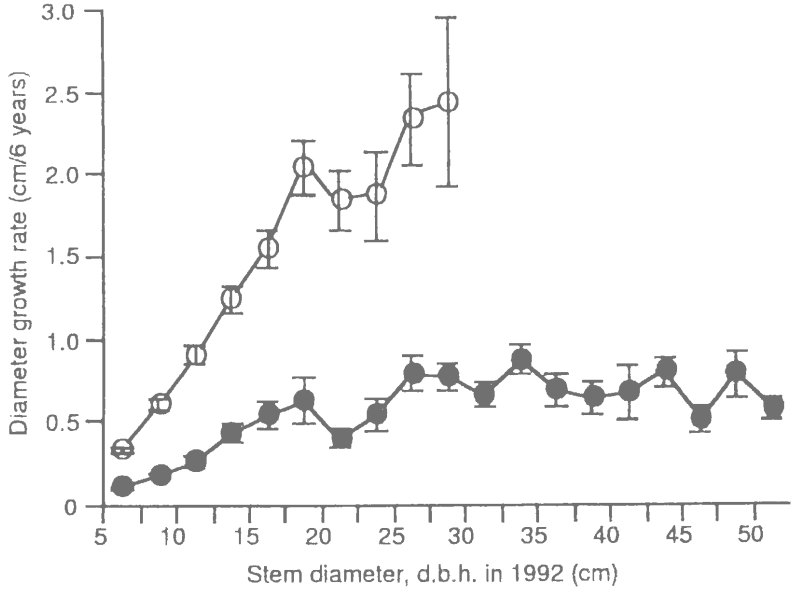

Fig. 4.7. Relationship between d.b.h. (stem diameter at breast height, 130 cm) in 1992 and absolute growth rate of stem diameter from 1992 to 1998 in the 40 m × 280 m plot at Mt. Mikasa, Nara City, Japan. Solid and open circles represent the rates in each d.b.h. class of *Podocarpus nagi* and *Neolitsea aciculata*, respectively. Bars indicate standard errors.

The growth rate of *P. nagi* trees, in the 5 ≤ d.b.h. < 10 cm class, was significantly dependent on their size ($P < 0.001$, Table 4.3) and was negatively correlated with the local crowding of *N. aciculata* ($P < 0.001$). In the 10 ≤ d.b.h. < 15 cm class, there was no significant partial correlation with tree size and local crowding of neighbouring trees. In the 15 ≤ d.b.h. < 30 cm class, the growth rate was negatively correlated with local crowding of *P. nagi* ($P < 0.01$). In the d.b.h. ≥ 30 cm class, there was no significant partial correlation with tree size and local crowding of neighbouring trees.

The growth rate of *N. aciculata* trees, in the 5 ≤ d.b.h. < 10 cm class, was significantly dependent on their size ($P < 0.001$, Table 4.3) and was negatively correlated with local crowding of *P. nagi* ($P < 0.05$) and of *N. aciculata* ($P < 0.01$). In the 10 ≤ d.b.h. < 15 cm class, the growth rate was positively correlated with the tree size

($P < 0.05$) and negatively correlated with local crowding of *P. nagi* ($P < 0.01$) and of *N. aciculata* ($P < 0.01$). In the d.b.h. ≥ 15 cm class, the growth rate was negatively correlated with the local crowding of *N. aciculata* ($P < 0.01$) and positively correlated with the local crowding of the other species ($P < 0.05$).

Table 4.3. Partial correlations of absolute growth rate (cm/6 years) of stem diameter with tree size in d.b.h. and local crowdings of *Podocarpus nagi*, *Neolitsea aciculata* and the other species trees in the 30 m × 270 m subplot at Mt. Mikasa, Nara City, Japan. Local crowding was calculated as the sum of basal area of the neighbouring trees within 5 m from a target tree. Assuming a one-sided competition, basal area was summed by trees with larger d.b.h. than a target tree. *n* is the number of trees. Bar indicates that all *N. aciculata* trees with d.b.h. ≥ 30 cm died by 1998. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, n.s. $P \geq 0.05$

		Partial correlation coefficient			
	n	D.b.h. in 1992	Local crowding of *P. nagi*	Local crowding of *N. aciculata*	Local crowding of other species
Podocarpus nagi					
5 ≤ d.b.h. < 10 cm	473	0.183 ***	n.s.	–0.174 ***	n.s.
10 ≤ d.b.h. < 15 cm	92	n.s.	n.s.	n.s.	n.s.
15 ≤ d.b.h. < 30 cm	133	n.s.	–0.274 **	n.s.	n.s.
d.b.h. ≥ 30 cm	145	n.s.	n.s.		n.s.
Neolitsea aciculata					
5 ≤ d.b.h. < 10 cm	528	0.387 ***	–0.104 *	–0.180 ***	n.s.
10 ≤ d.b.h. < 15 cm	200	0.177 *	–0.217 **	–0.198 **	n.s.
d.b.h. ≥ 15 cm	66	n.s.	n.s.	–0.333 **	0.282 *

Discussion

Patch formation of Podocarpus nagi *and* Neolitsea aciculata

The clumped distribution of *P. nagi* and *N. aciculata* trees and their spatial repulsion indicated that the observed forest consisted of patches dominated by either *P. nagi* or *N. aciculata*. The clumped distribution of plants could be caused by the dispersal ability and post-dispersal mortality of propagules. The narrow dispersal range of propagules created clumps of young plants (Sterner *et al.* 1986; Hatton 1989). If favourable sites for the survival and growth of dispersed propagules were spatially limited, the spatial

distribution of old or large plants was clumped (Williamson 1975, Rebertus *et al.* 1989).

Podocarpus nagi trees were less clumped with increasing tree size (Fig. 4.3). Such a shift was interpreted as a result of density-dependant mortality by intraspecific competition (Laessle 1965; Sterner *et al.* 1986; Kenkel 1988; Duncan 1991; Kenkel *et al.* 1997; Fulé & Covington 1998), although no significant change in spatial pattern of *P. nagi* population was detected for 6 years likely due to low mortality. In Chapter 2, it was reported that clumps of young *P. nagi* plants were caused by the narrow seed dispersal range and reproductive system (dioecy). A patch structure of *P. nagi* population was created by seed dispersal ability rather than by post-dispersal mortality.

Neolitsea aciculata trees were more clumped with increasing tree size (Fig. 4.4) and a significant increase in clumping intensity was observed for 6 years (Table 4.2). Briggs & Gibson (1992) observed that for three species, the distribution became more clumped with increasing tree height, and they suggested that differential mortality of juveniles may promote clumping. However, few studies have actually detected an increase in clumping intensity. Rebertus *et al.* (1989) observed an increase in clumping intensity of *Quercus laevis* due to mortality by fire. Peterson & Squiers (1995b) reported that the spatial distribution of aspen trees shifted to a more clumped distribution after 10 years and they attributed the shift to a clonal nature of aspen and competition. In our study, the observed increase in clumping intensity of *N. aciculata* might be caused by interspecific competition.

The increase in clumping intensity suggested that the patch structure of *N. aciculata* was created by the post-dispersal mortality rather than by the seed dispersal ability. Mortality and growth of *N. aciculata* might be affected by the local crowding of neighbouring *P. nagi* trees. An increase in the degree of repulsion of *N. aciculata* from *P. nagi* with increasing tree size (Fig. 4.5) suggested that the survival and growth of *N. aciculata* were facilitated where *P. nagi* trees were uncommon and interspecific competition was therefore less intense. In Chapter 2, it was reported that the spatial distribution of seedlings of *N. aciculata* did not depend on the location of seed sources (female trees) due to the wide seed dispersal range and did not depend on the spatial distribution of *P. nagi* trees. However, in this study, *N. aciculata* trees in the smallest size class ($5 \leq$ d.b.h. < 10 cm) were clumped and showed a repulsion from *P. nagi* trees. The exclusion of *N. aciculata* saplings due to the high density of neighbouring *P. nagi* might have proceeded by the time *N. aciculata* saplings grew larger than d.b.h. ≥ 5 cm.

Relative importance of intra- and interspecific competition

We assumed a one-sided competition for the analysis of the competitive effects of neighbours on the growth rate. The growth rate of both species trees significantly depended on their size (Table 4.3). The dependence of growth rate on tree size was more conspicuous in *N. aciculata* than in *P. nagi* (Fig. 4.7 and Table 4.3). The size dependence of growth rate suggested that large trees suppressed small trees but not vice versa, and competition was one-sided (Ford & Diggle 1981; Duncan 1991). The hypothesis of one-sided competition was also supported by the higher mortality rates of small trees than large trees (Fig. 4.6).

Kubota & Hara (1995, 1996) presented a process of habitat segregation based on competition between the saplings of two conifers, *Picea jezoensis* and *Abies sachalinensis*. They reported that an intense interspecific competition in the early stage of life-history brought about habitat segregation between the two species and interspecific competition became weaker in the adult stage. In our study, the relative importance of intraspecific competition to interspecific competition increased with the life-history stage from small trees to large trees (Table 4.3). Interspecific competition was significantly effective on the growth rate in small size classes, *P. nagi* trees in the $5 \leq$ d.b.h. < 10 cm class and *N. aciculata* trees in the $5 \leq$ d.b.h. < 10 cm and $10 \leq$ d.b.h. < 15 cm classes. However, only intraspecific competition had a significant effect on the growth rate in large size classes, *P. nagi* trees in the $15 \leq$ d.b.h. < 30 cm class and *N. aciculata* trees with d.b.h. ≥ 15 cm. The shift between inter- and intraspecific competitions corresponded to the change in spatial interaction between the two species. The more repulsive distribution with proceeding life-history stage indicated that, for both *P. nagi* and *N. aciculata*, the relative dominance of other species in neighbouring trees became lower with increasing tree size. Thus, the interspecific competition became weaker depending on the shift of spatial interactions between the two species, suggesting that the intra- and interspecific competitions and spatial patterns are interdependent.

Coexistence mechanism of **Podocarpus nagi** *and* **Neolitsea aciculata**

Podocarpus nagi and *Neolitsea aciculata* were codominant at Mt. Mikasa (Chapter 2; this chapter), although Koshimizu *et al.* (1971) and Suganuma & Kawai (1978) predicted that *P. nagi* would replace all the native tree species by its superior shade tolerance. In Chapter 2, spatial patterns of the two species at one time were analysed and it was

suggested that regeneration of *N. aciculata* was facilitated in the area where the density of *P. nagi* was low. A spatial refuge (Silvertown & Lovett Doust 1993) of *N. aciculata* (inferior competitor) from *P. nagi* (superior competitor) may enable coexistence of the two species.

As the distribution of species shifts toward a more clumped distribution, interspecific competition becomes less intense and intraspecific competition becomes more intense and a spatial refuge from competitors can be provided, because only the individuals on the edge of a monospecific clump compete with other species (Silvertown & Lovett Doust 1993). If the process proceeds to the point where intraspecific competition is stronger than interspecific competition for all competitors, the conditions for coexistence could be met (Shmida & Ellner 1984). *Neolitsea aciculata* trees became a more clumped and more repulsive from *P. nagi* trees with increasing tree size, and the mortality pattern toward a more clumped distribution was observed in *N. aciculata*. As the tree size of *P. nagi* and *N. aciculata* increased, the relative importance of interspecific competition became lower and that of intraspecific competition became higher. The effect of interspecific competition was not observed for *N. aciculata* with d.b.h. ≥ 15 cm. This indicated that the degree of repulsion between *N. aciculata* with d.b.h. ≥ 15 cm and *P. nagi* was sufficiently high for avoidance of interspecific competition. Duncan (1991) suggested that two dominant species in a mixed podocarp stand, *Dacrycarpus dacrydioides* and *Dacrydium cupressinum*, avoided interspecific competition by partitioning of the establishment site and concluded that the partitioning of sites may permit the coexistence of the two species. Our results of spatial and competitive interactions between the two species supported the coexistence mechanism proposed in Chapter 2 that the regeneration niche (Grubb 1977) for *N. aciculata* might be created by a combination of the clumped population structure of *P. nagi* and the wide seed dispersal range of *N. aciculata*.

Chapter 5

General Discussion – A model for coexistence of *Podocarpus nagi* and *Neolitsea aciculata*

Podocarpus nagi invaded Mt. Mikasa and replaced the native species. The species composition in the plot was completely different from that in the native forest adjacent to Mt. Mikasa (Nakane 1975; Suganuma & Kawai 1978; Naka 1982). Koshimizu *et al.* (1971) and Suganuma & Kawai (1978) considered that *P. nagi* eliminated all other species and monodominated the invaded area. In the study plot, however, *P. nagi* and *N. aciculata* were codominant (Chapter 2 and Chapter 4). Can the two species continue to coexist?

A transition matrix model for forest dynamics

A tree-by-tree replacement model has been used to predict forest dynamics (e.g. Horn 1975, Acevedo L. 1981). This model was represented by a transition matrix with elements p_{ij} which are probabilities that a tree of species i will replace a tree of species j. To examine effects of seed dispersal ability and dioecy on the competition between *P. nagi* and *N. aciculata*, and to discuss the probability of coexistence of the two species, a tree-by-tree replacement model was proposed (Fig. 5.1). The model is based on the following assumptions in the view of the results presented in preceding chapters: (1) The forest is composed of areas that can be allocated to one of three phases based on the canopy trees, i.e., female *P. nagi* is dominant in the F-phase, male *P. nagi* in the M-phase and *N. aciculata* in the N-phase (Chapter 2 and Chapter 4). The proportion of each area in the forest is f_F, f_M and f_N, respectively; (2) Sex ratio of *P. nagi* is unity (Chapter 2 and Chapter 3); (3) The F-phase is replaced by a canopy tree of *P. nagi* (Chapter 2 and Chapter 4); (4) The proportion of the M-phase or the N-phase replaced by a canopy tree of *P. nagi* is r. The value of r is proportional to the value of f_F, i.e., $r = kf_F$. The k is a constant and an index of dispersal ability of *P. nagi*; and (5) Seedlings of *N. aciculata* occur in all three phases and canopy trees of *N. aciculata* replace the phases that are not replaced by *P. nagi* (Chapter 2 and Chapter 4).

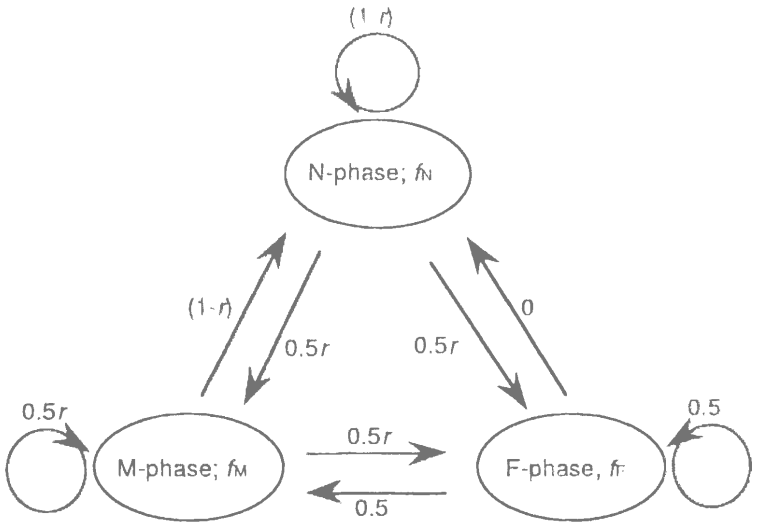

Fig. 5.1. Schematic diagram of regeneration patterns in *Podocarpus nagi* and *Neolitsea aciculata*. Direction of replacement in canopy trees is shown by arrows. The forest is composed of areas that can be allocated to one of three phases based on the canopy trees, i.e., female *P. nagi* is dominant in the F-phase, male *P. nagi* in the M-phase and *N. aciculata* in the N-phase. The proportion of each phase in the forest is f_F, f_M and f_N, respectively ($f_F + f_M + f_N = 1$). Sex ratio of *P. nagi* is unity. The F-phase is replaced by a canopy tree of *P. nagi*. The proportion of the M-phase or the N-phase replaced by a canopy tree of *Podocarpus nagi* is r. The value of r is proportional to the value of f_F, i.e., $r = kf_F$ (k is a constant). Canopy trees of *N. aciculata* replace the phases that are not replaced by *P. nagi*. Values by arrows represent transition probabilities of canopy trees per unit time.

Transition probabilities of three phases based on these assumptions are shown as equation 1 and the proportion of each area at time $t + 1$ is predicted by the values of f_F, f_M and f_N at time t as equation 2:

$$\begin{bmatrix} f_{F,t+1} \\ f_{M,t+1} \\ f_{N,t+1} \end{bmatrix} = \begin{bmatrix} 0.5 & 0.5r & 0.5r \\ 0.5 & 0.5r & 0.5r \\ 0 & 1-r & 1-r \end{bmatrix} \begin{bmatrix} f_{F,t} \\ f_{M,t} \\ f_{N,t} \end{bmatrix} \qquad \text{eqn 1}$$

$$f_{F,t+1} = 0.5f_{F,t} + 0.5rf_{M,t} + 0.5rf_{N,t}, \qquad \text{eqn 2a}$$

$$f_{M,t+1} = 0.5f_{F,t} + 0.5rf_{M,t} + 0.5rf_{N,t}, \qquad \text{eqn 2b}$$

$$f_{N,t+1} = (1-r)f_{M,t} + (1-r)f_{N,t}, \qquad \text{eqn 2c}$$

where $f_{F,t+1}$, $f_{M,t+1}$ and $f_{N,t+1}$ are proportions of the F-phase, the M-phase and the N-phase at time $t + 1$, respectively, and $f_{F,t}$, $f_{M,t}$ and $f_{N,t}$ are proportions of the F-phase, the M-phase and the N-phase at time t, respectively.

Based on the assumption (1),

$$f_F + f_M + f_N = 1 \qquad \text{eqn 3}$$

Based on the assumption (2),

$$f_F = f_M \qquad \text{eqn 4}$$

Based on the assumption (4),

$$r = kf_F, \qquad \text{eqn 5}$$

a constant, k, indicate a degree of the dispersal ability of *P. nagi*.

Using equations 3, 4 and 5, equations 2a, 2b and 2c can be rewritten by one equation represented by f_F as equation 6:

$$f_{F,t+1} = -0.5kf_{F,t}(f_{F,t} - \frac{1}{k} - 1) \qquad \text{eqn 6}$$

The equation 6 represents the proportion of the F-phase in the forest. The proportion of the areas dominated by canopy trees of *P. nagi*, i.e. the sum of the F-phase and the M-phase, is defined as f_{F+M}:

$$f_{F+M} = f_F + f_M \qquad \text{eqn 7}$$

Using equations 4, 6 and 7, f_{F+M} is represented as equation 8:

$$f_{F+M,t+1} = -0.25kf_{F+M,t}(f_{F+M,t} - \frac{2}{k} - 2) \qquad \text{eqn 8}$$

Probability of coexistence of Podocarpus nagi *and* Neolitsea aciculata

Since it is assumed that all areas are occupied by *P. nagi* and *N. aciculata* (assumption (1)), the forest dynamics is specified by the behaviour of f_{F+M} through time (Fig. 5.2). When $k \leq 1$, the stable equilibrium point of f_{F+M} value (f^*_{F+M}) is 0 (Fig. 5.2a). This result indicates the extinction of the *P. nagi* population. When $k \geq 2$, the stable equilibrium point of f_{F+M} value is 1 (Fig. 5.2c). This result indicates the extinction of the *N. aciculata* population. When $1 < k < 2$, the stable equilibrium point is $f^*_{F+M} = 2 - 2/k$ and $0 < f^*_{F+M} < 1$ (Fig. 5.2b). This result indicates the stable coexistence of *P. nagi* and *N. aciculata*. These results are not dependent on initial values of f_{F+M}. The transition matrix model supported the hypothesis that the two species can coexist by trade-off between competitive ability and dispersal ability and by dioecy of *P. nagi*, when $1 < k < 2$.

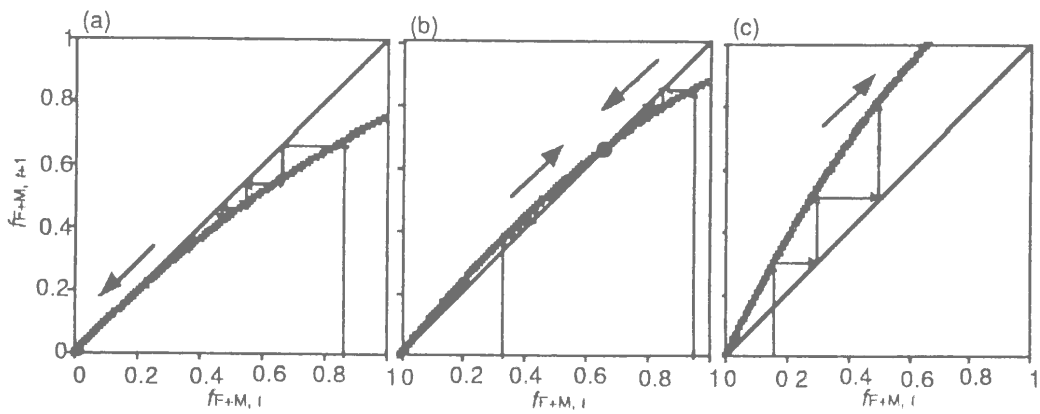

Fig. 5.2. Stable equilibrium obtained by (a) $k \leq 1$, (b) $1 < k < 2$ and (c) $k \geq 2$. Values of f_{F+M} represent the proportion of areas dominated by canopy trees of *Podocarpus nagi* at an arbitrary time, t.

Effects of sex ratio of Podocarpus nagi *on forest dynamics*

Based on the assumption that sex ratio of *P. nagi* is unity, *P. nagi* and *N. aciculata* can coexist when $1 < k < 2$. In this section, the author will examine the influence of sex ratio of *P. nagi* on the coexistence of the two species.

The female ratio (female/(female + male)) in the *P. nagi* population is defined as R_F ($0 < R_F < 1$). Transition probabilities of three phases are shown as equation 9 and the

proportion of each area at time $t + 1$ is predicted by the values of f_F, f_M and f_N at time t as equation 10.

$$\begin{bmatrix} f_{F,t+1} \\ f_{M,t+1} \\ f_{N,t+1} \end{bmatrix} = \begin{bmatrix} R_F & R_F r & R_F r \\ (1-R_F) & (1-R_F)r & (1-R_F)r \\ 0 & 1-r & 1-r \end{bmatrix} \begin{bmatrix} f_{F,t} \\ f_{M,t} \\ f_{N,t} \end{bmatrix} \quad \text{eqn 9}$$

$$f_{F,t+1} = R_F f_{F,t} + R_F r f_{M,t} + R_F r f_{N,t} \quad \text{eqn 10a}$$

$$f_{M,t+1} = (1 - R_F) f_{F,t} + (1 - R_F) r f_{M,t} + (1 - R_F) r f_{N,t} \quad \text{eqn 10b}$$

$$f_{N,t+1} = (1 - r) f_{M,t} + (1 - r) f_{N,t} \quad \text{eqn 10c}$$

At equilibrium point, $f_{F,t+1} = f_{F,t} = f^*_F$, $f_{M,t+1} = f_{M,t} = f^*_M$ and $f_{N,t+1} = f_{N,t} = f^*_N$. Therefore, equation 10 is rewritten as equation 11.

$$f^*_F = R_F f^*_F + R_F r f^*_M + R_F r f^*_N \quad \text{eqn 11a}$$

$$f^*_M = (1 - R_F) f^*_F + (1 - R_F) r f^*_M + (1 - R_F) r f^*_N \quad \text{eqn 11b}$$

$$f^*_N = (1 - r) f^*_M + (1 - r) f^*_N \quad \text{eqn 11c}$$

Using equations 3, 5 and a condition that females and males of *P. nagi* are in the ratio of $R_F : (1 - R_F)$, equation 11 can be rewritten by k and R_F as equation 12.

$$f^*_F = \frac{1}{k} + 1 - \frac{1}{kR_F} \quad \text{eqn 12a}$$

$$f^*_M = \frac{2}{kR_F} + \frac{1}{R_F} - \frac{1}{kR_F^2} - \frac{1}{k} - 1 \quad \text{eqn 12b}$$

$$f^*_N = 1 - \frac{1}{kR_F} - \frac{1}{R_F} + \frac{1}{kR_F^2} \quad \text{eqn 12c}$$

The proportion of the areas dominated by canopy trees of *P. nagi*, i.e. the sum of the F-phase and the M-phase ($f^*_F + f^*_M$), is represented as equation 13.

$$f^*_{F+M} = \frac{1}{kR_F} + \frac{1}{R_F} - \frac{1}{kR_F^2} \quad \text{eqn 13}$$

When $0 < f^*_{F+M} < 1$, *P. nagi* and *N. aciculata* coexist. This occurs when $1/R_F - 1 < k < 1/R_F$ (Fig. 5.3). When $k \geq 1/R_F$, the value of f^*_{F+M} is 1 and the value of f^*_N is 0. This indicates that *P. nagi* exclude *N. aciculata* (Fig. 5.3). When $k \leq 1/R_F - 1$, the value f^*_{F+M} value is 0 and the value of f^*_N is 1. This indicates that *N. aciculata* exclude *P. nagi* (Fig. 3).

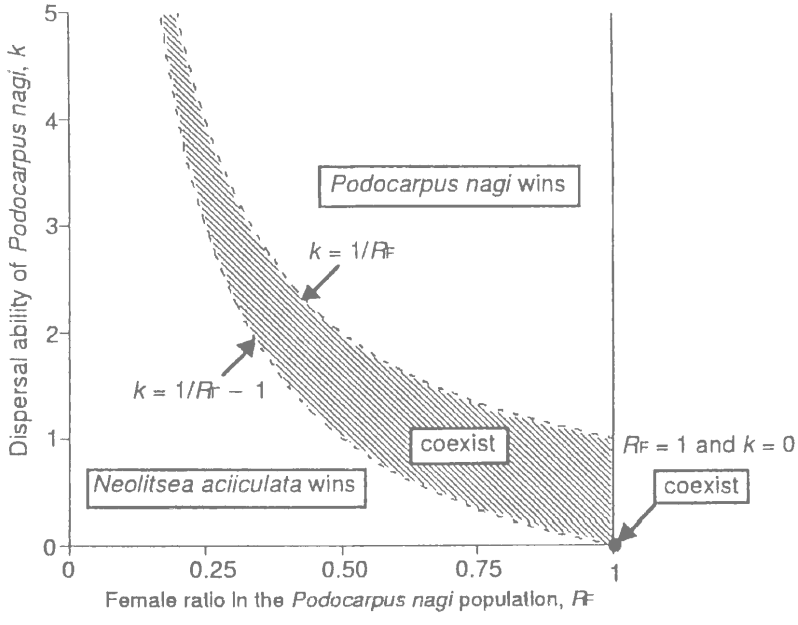

Fig. 5.3. Dependence of the stable equilibrium state of a *Podocarpus nagi* and *Neolitsea aciculata* system on two model parameters, R_F and k. If the sex expression of *P. nagi* is dioecy ($0 < R_F < 1$), the two species coexist if $1/R_F - 1 < k < 1/R_F$. If the sex expression of *P. nagi* is cosexual (e.g. hermaphrodite) ($R_F = 1$), the two species can coexist only when $k = 0$.

Effects of dioecy of Podocarpus nagi *on forest dynamics*

If the sex expression of *P. nagi* is cosexual (e.g. hermaphrodite), all *P. nagi* trees can produce seeds, therefore, the forest is composed of two phases, i.e., the F-phase and the N-phase. Transition probabilities of three phases are shown as equation 14 and the proportion of each area at time $t + 1$ is predicted by the values of f_F and f_N at time t as equation 15.

$$\begin{bmatrix} f_{F,t+1} \\ f_{N,t+1} \end{bmatrix} = \begin{bmatrix} 1 & r \\ 0 & 1-r \end{bmatrix} \begin{bmatrix} f_{F,t} \\ f_{N,t} \end{bmatrix} \qquad \text{eqn 14}$$

$f_{F,t+1} = f_{F,t} + rf_{N,t}$ eqn 15a

$f_{N,t+1} = (1 - r)f_{N,t}$ eqn 15b

At equilibrium point, $f_{F,t+1} = f_{F,t} = f^*_F$ and $f_{N,t+1} = f_{N,t} = f^*_N$. Therefore, using equation 5, equation 15 is rewritten as equation 16.

$f^*_F = f^*_F + kf^*_F f^*_N$ eqn 16a

$f^*_N = f^*_N - kf^*_F f^*_N$ eqn 16b

Equation 16 indicates $kf^*_F f^*_N = 0$. This is materialized when $f^*_F = 0$ or $f^*_N = 0$ or $k = 0$. The condition, $f^*_F = 0$ or $f^*_N = 0$, implies the extinction of *P. nagi* or *N. aciculata*, respectively. Therefore, the two species can coexist only when $k = 0$ (Fig. 5.3), i.e., *P. nagi* trees replace only the F-phase. This implies that, if *P. nagi* trees can replace the N-phase a little, *N. aciculata* is gradually excluded by *P. nagi* even though *N. aciculata* has a superior dispersal ability than *P. nagi*. Therefore, the two species can not coexist only by the trade-off between competitive ability and dispersal ability.

There are two effects of dioecy on the regeneration pattern of *P. nagi*. One is the decrement of seed-dispersed area throughout the forest (an increment of spatial heterogeneity of dispersed seed density throughout the forest). The other is the increment of spatial heterogeneity of the seed density in the area where the large *P. nagi* trees are dominant (the creation of two phases with a different density of young plants, i.e., F-phase and M-phase). In the case of cosexual (e.g. hermaphrodite) species, they had only one phase. Dioecy caused a quantitative (coefficient of variance) and qualitative (number of modes) increase in spatial heterogeneity of the seed density. The creation of qualitative increase, i.e., two phases of dispersed seed density, enables the coexistence of *P. nagi* and *N. aciculata*.

Causes of gaps for regeneration of Neolitsea aciculata

Grubb (1977) proposed the regeneration niche for the coexistence of two species, suggesting that, if species A tends to oust species B, necessary conditions were either the creation of a gap which favours the establishment of B more than A or the creation of a gap at a place where B has propagules and A has not. Hanski & Ranta (1983) reported species coexistence is possible by a trade-off between competitive ability and dispersal ability and by creation of empty areas of competitors. Our results suggested that the male

P. nagi trees continued to create a gap for the regeneration of *N. aciculata*. Grubb (1977) listed factors creating gaps; fire, cyclone, constant winds, and the fall of single trees or branches. These factors create 'canopy gaps' and change environmental conditions suddenly (i.e. disturbance, Sprugel 1976; Runkle 1981; Romme 1982; White & Pickett 1985). Our study suggests that a male *P. nagi* tree can gradually create a gap which decreases the density of *P. nagi* around the male *P. nagi* trees. This 'competitor gap' favours the growth and reproduction of *N. aciculata*. The regeneration niche for *N. aciculata* can be guaranteed by the competitor gap created by male *P. nagi* trees accounting for 50% or more fraction of reproductive *P. nagi* trees and wide seed dispersal range of *N. aciculata*. The creation of the gap for regeneration of *N. aciculata* may be caused by the population structure of *P. nagi* itself without any disturbance.

Summary

Chapter 1

Species coexistence in plant communities has been a subject of ecological research. For understanding species richness in plant communities, a plant-by-plant replacement process is important, and this process is affected by biological interactions among plants. This study aims to reveal the regeneration dynamics of a forest community dominated by two dioecious tree species, *Podocarpus nagi* and *Neolitsea aciculata*, and to discuss the coexistence mechanism of the two species, focusing on sex expression (dioecy), seed dispersal ability and intra- and interspecific competition of the two species. The author hypothesized that (1) seed dispersal in *P. nagi* is limited to the area around female trees; (2) the density of young plants of *P. nagi* become high in the area around female trees but low in the area around male trees; (3) seed dispersal of *N. aciculata* is sufficient to occur at any point within the forest; and (4) the regeneration of *N. aciculata* is facilitated where *P. nagi* plants are uncommon and competition is therefore less intense.

Chapter 2

Spatial patterns of two codominant dioecious tree species, *Podocarpus nagi* and *Neolitsea aciculata*, were analysed at Mt. Mikasa, Nara City, Japan. *Podocarpus nagi* has a higher shade tolerance than *N. aciculata*, while it has a narrower seed dispersal range than *N. aciculata*. The author examined the effects of dioecy on regeneration and coexistence of the two species. Large seeds (10–15 mm in diameter) of *P. nagi* were dispersed by gravity only around female trees. Young plants of *P. nagi* were clumped and showed a significant attraction to large female trees and a significant repulsion from large male trees. Dioecy affected the spatial heterogeneity of plant density in the *P. nagi* population. Young plants of *N. aciculata* showed no significant attraction to female trees because seeds of *N. aciculata* were widely dispersed by birds. The wide seed-dispersal moderated the effects of dioecy on the spatial pattern in *N. aciculata*. Large *N.aciculata* trees were clumped and showed a significant attraction to large male *P. nagi* trees. The results of spatial analyses suggest that the growth of *N. aciculata* is facilitated around large male *P. nagi* trees, in which competition is less intense since young *P. nagi* plants are uncommon. This study suggests that the dioecy-induced population structure of *P. nagi* can promote the coexistence of *P. nagi* and *N. aciculata*.

Chapter 3

Sex ratio, size structure and spatial pattern of a dioecious tree species, *Podocarpus nagi*, were analysed according to size class at Mt. Mikasa, Nara City, Japan. The roles of life history traits on the formation of the sex-related population structure were discussed. The sex ratio of reproductive trees larger than 5 cm in stem diameter at breast height (d.b.h., 130 cm above ground level) was significantly male-biased. The sex ratio was male-biased in $5 \leq$ d.b.h. < 20 cm class and d.b.h. ≥ 50 cm class, while in $20 \leq$ d.b.h. < 50 cm class the sex ratio did not depart from 1:1. The growth rate varied with tree size for males but not for females. Males showed a lower growth rate than females in $5 \leq$ d.b.h. < 20 cm class, although the number of males with high growth rates was significantly large in d.b.h. ≥ 20 cm class. Precocity and vigour of males suggested that differences in reproductive cost between sexes induced the biased sex ratio. Males and females were clumped and showed a significant attraction to each other in $5 \leq$ d.b.h. < 30 cm class. In d.b.h. ≥ 30 cm class, males showed a clumped distribution, whereas females showed a random distribution and males and females showed a significant repulsion against each other. Growth rate of females was negatively correlated with both local crowding of males and females, whereas growth rate of males did not show any significant correlation with local crowding of neighbours. Females suffered more than males from the presence of neighbours, suggesting that sexual difference of competitive ability was related with the formation of gender-dependent spatial patterns. Formation of female-repulsive male clumps and male-biased sex ratio may intensify the decrease in probability of regeneration around males, proposed by the narrow seed dispersal range of *P. nagi*, and may promote the coexistence with other codominant species.

Chapter 4

Spatial patterns, changes in spatial patterns due to mortality, and intra- and interspecific competitions of two codominant dioecious tree species, *Podocarpus nagi* and *Neolitsea aciculata*, were analysed at Mt. Mikasa, Nara City, Japan. *Podocarpus nagi* has a higher shade tolerance but a narrower seed dispersal range than *N. aciculata*. We inferred the mechanisms of patch formation and coexistence of the two species. *Podocarpus nagi* and *N. aciculata* trees were clumped and showed a spatial repulsion from each other. Patches dominated by either *P. nagi* or *N. aciculata* were formed. *Podocarpus nagi* trees were less clumped with increasing tree size, although no significant change in spatial patterns

due to mortality was detected for 6 years. A patch formation of the *P. nagi* population was induced by the narrow seed dispersal range and dioecy rather than by post-dispersal mortality. *Neolitsea aciculata* trees were more clumped and more repulsive from *P. nagi* trees with increasing tree size. The distribution of small *N. aciculata* trees living in 1998 was significantly more clumped than that expected from the random mortality of trees living in 1992. Post-dispersal mortality due to interspecific competition (competitive exclusion by *P. nagi*) affected the patch formation of the *N. aciculata* population. The relative importance of intraspecific competition to interspecific competition on the growth rate increased with the life-history stage from small trees to large trees. The shift corresponded to an increasing spatial repulsion between the two species. Interdependence of spatial and competitive interactions between the two species was suggested. The patch formation of *P. nagi* population may create the spatial refuge of *N. aciculata* from *P. nagi* and may enable avoidance of interspecific competition and the coexistence of the two species.

Chapter 5

To discuss the coexistence mechanism of *Podocarpus nagi* and *Neolitsea aciculata*, a tree-by-tree replacement model was proposed. The model is based on the assumption that the forest is composed of areas that can be allocated to one of three phases based on the canopy trees, i.e., female *P. nagi* is dominant in the F-phase, male *P. nagi* in the M-phase, and *N. aciculata* in the N-phase. The proportion of the M-phase or the N-phase replaced by a canopy tree of *P. nagi*, r, determined whether the two species coexist or not. The values of r that enable coexistence of the two species was dependent on the sex ratio of *P. nagi*. The model suggested that the coexistence of the two species was promoted not only by a trade-off between the greater shade tolerance of *P. nagi* and the superior seed dispersal ability of *N. aciculata* but also by a dioecy of *P. nagi*. The model suggests that the regeneration niche for *N. aciculata* can be guaranteed by the 'competitor gap' created by male *P. nagi* trees accounting for 50% or more fraction of reproductive *P. nagi* trees and wide seed dispersal range of *N. aciculata*. The creation of the gap for regeneration of *N. aciculata* may be caused by the population structure of *P. nagi* itself without any disturbance.

References

Abbott, I. (1984) Comparisons of spatial pattern, structure, and tree composition between virgin and cut-over jarrah forest in western Australia. *Forest Ecology and Management*, **9**, 101-126.

Acevedo L., M.F. (1981) On Horn's Markovian model of forest dynamics with particular reference to tropical forests. *Theoretical Population Biology*, **19**, 230–250.

Ackerly, D.D., Rankin-de-Merona, J.M. & Rodrigues, W.A. (1990) Tree densities and sex ratios in breeding populations of dioecious Central Amazonian Myristicaceae. *Journal of Tropical Ecology*, **6**, 239–248.

Aiba, S. & Kohyama, T. (1997) Crown architecture and life-history traits of 14 tree species in a warm–temperate rain forest: significance of spatial heterogeneity. *Journal of Ecology*, **85**, 611–624.

Allen, G.A. & Antos, J.A. (1993) Sex ratio variation in the dioecious shrub *Oemleria cerasiformis*. *American Naturalist*, **141**, 537–553.

Alliende, M.C. & Harper, J.L. (1989) Demographic studies of a dioecious tree. I Colonization, sex and age structure of a population of *Salix cinerea*. *Journal of Ecology*, **77**, 1029–1047.

Andersen, M. (1992) Spatial analysis of two-species interactions. *Oecologia*, **91**, 134–140.

Antonovics, J. & Levin, D.A. (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*, **11**, 411–452.

Armesto, J.J., Pickett, S.T.A. & McDonnell, M.J. (1991) Spatial heterogeneity during succession: a cyclic model of invasion and exclusion. *Ecological Heterogeneity* (eds J. Kolasa & S.T.A. Pickett), pp. 256–269. Springer-Verlag, New York.

Augspurger, C.K. (1983) Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology*, **71**, 759–771.

Besag, J. (1977) Contribution to the discussion on Dr Ripley's paper. *Journal of the Royal Statistical Society B*, **39**, 193–195.

Besag, J. & Diggle, P.J. (1977) Simple Monte Carlo tests for spatial pattern. *Applied Statistics*, **26**, 327–333.

Bierzychudek, P. & Eckhart, V. (1988) Spatial segregation of the sexes of dioecious

plants. *American Naturalist*, **132**, 34–43

Black, J.N. (1960) An assessment of the role of planting density in competition between red clover (*Trifolium pratense* L.) and lucerne (*Medicago sativa* L.) in the early vegetative stage. *Oikos*, **11**, 26–42.

Bockelmann, Anna-Christina & Neuhaus, R. (1999) Competitive exclusion of *Elymus athericus* from a high-stress habitat in a European salt marsh. *Journal of Ecology*, **87**, 503–513.

Brokaw, N.V.L. (1985) Treefall, regrowth, and community structure in tropical forests. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 53–69. Academic Press, New York.

Briggs, J.M. & Gibson, D.J. (1992) Effect of fire on tree spatial patterns in a tallgrass prairie landscape. *Bulletin of the Torrey Botanical Club*, **119**, 300–307.

Callaway, R.M. (1992) Effects of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology*, **73**, 2118–2128.

Christensen, N.L. (1977) Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. *American Midland Naturalist*, **97**, 176–188.

Clark, D.A. & Clark, D.B. (1987) Temporal and environmental patterns of reproduction in *Zamia skinneri*, a tropical rain forest cycad. *Journal of Ecology*, **75**, 135–149.

Condit, R., Hubbell, S.P. & Foster, R.B. (1994) Density dependence in two understory tree species in a neotropical forest. *Ecology*, **75**, 671–680.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (eds P.J. den Boer & G.R. Gradwell), pp. 298–312. Centre for Agricultural Publishing and Documentation, Wageningen.

Cox, P.A. (1981) Niche partitioning between sexes of dioecious plants. *American Naturalist*, **117**, 295–307.

Dale, M.R.T. (1999) *Spatial Pattern Analysis in Plant Ecology*. Cambridge University Press, Cambridge, UK.

Dalling, J.W., Hubbell, S.P. & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, **86**, 674–689.

Dawson, T.E. & Bliss, L.C. (1989) Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. *Oecologia*, **79**, 332–343.

Diggle, P.J. (1983) *Statistical Analysis of Spatial Point Patterns*. Academic Press London.

Duncan, R.P. (1991) Competition and the coexistence of species in a mixed podocarp stand. *Journal of Ecology*, **79**, 1073–1084.

Ford, E.D. & Diggle, P.J. (1981) Competition for light in a plant monoculture modelled as a spatial stochastic process. *Annals of Botany*, **48**, 481–500.

Forget, P.M. (1991) Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana. *Oecologia*, **85**, 434–439.

Fowler, N. (1986) The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89–110.

Freeman, D.C., Klikoff, L.G. & Harper, K.T. (1976) Differential resource utilization by the sexes of dioecious plants. *Science*, **193**, 597–599.

Frelich, L.E., Calcote, R.R. & Davis, M.B. (1993) Patch formation and maintenance in an old-growth hemlock–hardwood forest. *Ecology*, **74**, 513–527.

Frelich, L.E., Sugita, S., Reich, P.B., Davis, M.B. & Friedman, S.K. (1998) Neighbourhood effects in forests: implications for within-stand patch structure. *Journal of Ecology*, **86**, 149–161.

Fulé, P.Z. & Covington, W.W. (1998) Spatial patterns of Mexican pine-oak forests under different recent fire regimes. *Plant Ecology*, **134**, 197–209.

Gibson, D.J. & Menges, E.S. (1994) Population structure and spatial pattern in the dioecious shrub *Ceratiola ericoides*. *Journal of Vegetation Science*, **5**, 337–346.

Grant, M.C. & Mitton, J.B. (1979) Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolution*, **33**, 914–918.

Greig-Smith, P. (1979) Pattern in vegetation. *Journal of Ecology*, **67**, 755–779.

Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.

Grubb, P.J. (1986) Problems posed by sparse and patchily distributed species in species-rich plant commynities. *Community Ecology* (eds J. Diamond & T.J. Case), pp. 207–225. Harper & Row, New York.

Gurevitch, J. (1986) Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology*, **67**, 46–57.

Haase, P. (1995) Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. *Journal of Vegetation Science*, **6**, 575–582.

Haase, P., Pugnaire, F.I., Clark, S.C & Incoll, L.D. (1997) Spatial pattern in *Anthyllis cytisoides* shrubland on abandoned land in southeastern Spain. *Journal of Vegetation Science*, **8**, 627–634.

Hall, R.C. (1944) A vernier tree-growth band. *Journal of Forestry*, **42**, 742–743.

Hanski, I. & Ranta, E. (1983) Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *Journal of Animal Ecology*, **52**, 263–279.

Hara, T., Nishimura, N. & Yamamoto, S. (1995) Tree competition and species coexistence in a cool-temperate old-growth forest in southwestern Japan. *Journal of Vegetation Science*, **6**, 565–574.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London, UK.

Hart, T.B., Hart, J.A. & Murphy, P.G. (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *American Naturalist*, **133**, 613–633.

Hatton, T.J. (1989) Spatial analysis of a subalpine heath woodland. *Australian Journal of Ecology*, **14**, 65–75.

Herrera, C.M. (1988) Plant size, spacing patterns, and host-plant selection in *Osyris quadripartita*, a hemiparasitic dioecious shrub. *Journal of Ecology*, **76**, 995–1006.

Hoffmann, A.J. & Alliende, M.C. (1984) Interactions in the patterns of vegetative growth and reproduction in woody dioecious plants. *Oecologia*, **61**, 109–114.

Holthuijzen, A.M.A., Sharik, T.L. & Fraser, J.D. (1987) Dispersal of eastern red cedar (*Juniperus virginiana*) into pastures: an overview. *Canadian Journal of Botany*, **65**, 1092–1095.

Hoppes, W.G. (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology*, **69**, 320–329.

Horn, H.S. (1975) Markovian properties of forest succession. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 196–211. Harvard University Press, Cambridge, MA.

Houle, G. (1992) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *Journal of Ecology*, **80**, 99–108.

Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.

Hubbell, S.P. & Foster R.B. (1986) Canopy gaps and the dynamics of a neotropical forest. *Plant Ecology* (ed M.J. Crawley), pp. 77 -96. Blackwell Science, Oxford, UK.

Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.

Hutchinson, G.E. (1975) Variations on a theme by Robert MacArthur. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 492–521. Harvard University Press, Cambridge, MA.

Iglesias, M.C. & Bell, G. (1989) The small-scale spatial distribution of male and female plants. *Oecologia*, **80**, 229–235.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests *American Naturalist*, **104**, 501–528.

Jenkins, M.A. & Pallardy, S.G. (1995) The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Canadian Journal of Forest Research*, **25**, 1119–1127.

Kenkel, N.C. (1988) Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology*, **69**, 1017–1024.

Kenkel, N.C. (1993) Modeling markovian dependence in populations of *Aralia nudicaulis*. *Ecology*, **74**, 1700–1706.

Kenkel, N.C., Hendric, M.L. & Bella, I.E. (1997) A long-term study of *Pinus banksiana* population dynamics. *Journal of Vegetation Science*, **8**, 241–254.

Kohyama, T. (1991) Simulating stationary size distribution of trees in rain forests. *Annals of Botany*, **68**, 173–180.

Kohyama, T. (1992) Size-structured multi-species model of rain forest trees. *Functional Ecology*, **6**, 206–212.

Kohyama, T. (1993) Size-structured tree populations in gap-dynamic forest – the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology*, **81**, 131–143.

Kohyama, T. & Grubb, P.J. (1994) Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm–temperate rain forest. *Functional Ecology*, **8**, 229–236.

Koshimizu, T., Iwata, S., Suganuma, T., Kitagawa, N. & Hamada, M. (1971) Nature and history of Nara City. *Nature in Nara City* (ed. T. Koshimizu), pp. 109–260. Nara Municipal Office, Nara, Japan [in Japanese].

Kotanen, P.M. (1997) Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. *Canadian Journal of Botany*, **75**, 352–361.

Kubota, Y. & Hara, T. (1995) Tree competition and species coexistence in a sub-boreal

forest, northern Japan. *Annals of Botany*, **76**, 503–512.

Kubota, Y. & Hara, T. (1996) Allometry and competition between saplings of *Picea jezoensis* and *Abies sachalinensis* in a sub-boreal coniferous forest, northern Japan. *Annals of Botany*, **77**, 529–537.

Laessle, A.M. (1965) Spacing and competition in natural stands of sand pine. *Ecology*, **46**, 65–72.

Liming, F.G. (1957) Homemade dendrometers. *Journal of Forestry*, **55**, 575–577.

Lloyd, D.G. & Webb, C.J. (1977) Secondary sex characters in plants. *Botanical Review*, **43**, 177–216.

Lotwick, H.W. & Silverman, B.W. (1982) Methods for analysing spatial processes of several types of points. *Journal of the Royal Statistical Society B*, **44**, 406–413.

Lovett Doust, J. & Lovett Doust, L. (1988) Modules of production and reproduction in a dioecious clonal shrub, *Rhus typhina*. *Ecology*, **69**, 741–750.

Lusk, C. & Ogden, J. (1992) Age structure and dynamics of a podocarp–broadleaf forest in Tongariro National Park, New Zealand. *Journal of Ecology*, **80**, 379–393.

MacArthur, R.H. (1972) *Geographical Ecology*. Harper & Row, New York.

Mack, A.L. (1997) Spatial distribution, fruit production and seed removal of a rare, dioecious canopy tree species (*Aglaia* aff. *flavida* Merr. et Perr.) in Papua New Guinea. *Journal of Tropical Ecology*, **13**, 305–316.

Mack, R.N. & Harper, J.L. (1977) Interference in dune annuals: spatial pattern and neighbourhood effects. *Journal of Ecology*, **65**, 345–363.

Marino, P.C. (1991) Dispersal and coexistence of mosses (Splachnaceae) in patchy habitats. *Journal of Ecology*, **79**, 1047–1060.

Marriott, F.H.C. (1979) Barnard's Monte Carlo tests: How many simulations? *Applied Statistics*, **28**, 75–77.

Murray, K.G. (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, **58**, 271–298.

Naka, K. (1982) Community dynamics of evergreen broadleaf forests in southwestern Japan. I. Wind damaged trees and canopy gaps in an evergreen oak forest. *Botanical Magazine, Tokyo*, **95**, 385–399.

Nakane, K. (1975) Dynamics of soil organic matter in different parts on a slope under evergreen oak forest. *Japanese Journal of Ecology*, **25**, 206–216 (in Japanese with English summary).

Nakanishi, H. (1996) Fruit color and fruit size of bird-disseminated plants in Japan. *Vegetatio*, **123**, 207–218.

Nakashizuka, T. (1987) Regeneration dynamics of beech forests in Japan. *Vegetatio*, **69**, 169–175.

Nakashizuka, T. & Kohyama, T. (1995) The significance of the asymmetric effect of crowding for coexistence in a mixed temperate forest. *Journal of Vegetation Science*, **6**, 509–516.

Nicotra, A.B. (1998) Sex ratio variation and spatial distribution of *Siparuna grandiflora*, a tropical dioecious shrub. *Oecologia*, **115**, 102–113.

Noma, N. & Yumoto, T. (1997) Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research*, **12**, 119–129.

Obeso, J.R. (1997) Costs of reproduction in *Ilex aquifolium*: effects at tree, branch and leaf levels. *Journal of Ecology*, **85**, 159–166.

Ohmae, Y., Shibata, K. & Yamakura, T. (1996) Seasonal change in nagilactone contents in leaves in *Podocarpus nagi* forest. *Journal of Chemical Ecology*, **22**, 477–489.

Onyekwelu, S.S. & Harper, J.L. (1979) Sex ratio and niche differentiation in spinach (*Spinacia oleracea* L.). *Nature*, **282**, 609–611.

Opler, P.A. & Bawa, K.S. (1978) Sex ratios in tropical forest trees. *Evolution*, **32**, 812–821.

Pedersen, B.S. (1998) The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology*, **79**, 79–93.

Peterson, C.J. & Squiers, E.R. (1995a) Competition and succession in an aspen–white-pine forest. *Journal of Ecology*, **83**, 449–457.

Peterson, C.J. & Squiers, E.R. (1995b) An unexpected change in spatial pattern across 10 years in an aspen–white-pine forest. *Journal of Ecology*, **83**, 847–855.

Phillips, D.L. & MacMahon, J.A. (1981) Competition and spacing patterns in desert shrubs. *Journal of Ecology*, **69**, 97–115.

Pielou, E.C. (1977) *Mathematical Ecology*. John Wiley & Sons, New York.

Prentice, I.C. & Werger, M.J.A. (1985) Clump spacing in a desert dwarf shrub community. *Vegetatio*, **63**, 133–139.

Rebertus, A.J., Williamson, G.B. & Moser, E.B. (1989) Fire-induced changes in *Quercus laevis* spatial pattern in Florida sandhills. *Journal of Ecology*, **77**, 638–650.

Ripley, B.D. (1977) Modelling spatial patterns. *Journal of the Royal Statistical Society B*, **39**, 172–212.

Romme, W.H. (1982) Fire and landscape diversity in subalpine forests of Yellowstone

National Park. *Ecology*, **52**, 199–221.

Runkle, J.R. (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, **62**, 1041–1051.

Runkle, J.R. (1985) Disturbance regimes in temperate forests. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 17–33. Academic Press, Orlando, Florida.

Schupp, E.W., Howe, H.F., Augspurger, C.K. & Levey, D.J. (1989) Arrival and survival in tropical treefall gaps. *Ecology*, **70**, 562–564.

Shmida, A. & Ellner, S. (1984) Coexistence of plant species with similar niches. *Vegetatio*, **58**, 29–55.

Shimoda, K., Kimura, K., Kanzaki, M. & Yoda, K. (1994) The regeneration of pioneer tree species under browsing pressure of Sika deer in an evergreen oak forest. *Ecological Research*, **9**, 85–92.

Silvertown, J.W. & Lovett Doust, J. (1993) *Introduction to plant population biology*. Blackwell Science, Oxford, UK.

Silvertown, J. & Wilson, J.B. (1994) Community structure in a desert perennial community. *Ecology*, **75**, 409–417.

Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.

Society of Deer Conservation, Nara. (1994) Population statistics of deer. The Society of Deer Conservation, Nara (in Japanese).

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. W. H. Freeman and Company, New York, NY.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353–391.

Sprugel, D.G. (1976) Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *Journal of Ecology*, **64**, 889–911.

Sterner, R.W., Ribic, C.A. & Schatz, G.E. (1986) Testing for life historical changes in spatial patterns of four tropical tree species. *Journal of Ecology*, **74**, 621–633.

Stoll, P., Weiner, J. & Schmid, B. (1994) Growth variation in a naturally established population of *Pinus sylvestris*. *Ecology*, **75**, 660–670.

Suganuma, T. & Kawai, Y. (1978) Phytosociological study of *Podocarpus nagi* forest in the precincts of Kasuga Shrine, Nara. *The Journal of Geobotany*, **25**, 221–228 [in Japanese with English summary].

Takatsuki, S. (1989) Effects of deer on plants and plant communities. *Japanese Journal*

of Ecology, **39**, 67–80 (in Japanese with English summary).

Thomas, S.C. & Weiner, J. (1989) Including competitive asymmetry in measures of local interference in plant populations. *Oecologia*, **80**, 349–355.

Thomas, S.C. & LaFrankie, J.V. (1993) Sex, size, and interyear variation in flowering among dioecious trees of the Malayan rain forest. *Ecology*, **74**, 1529–1537.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Upton, G. & Fingleton, B. (1985) *Spatial Data Analysis by Example*, Vol. 1. *Point Pattern and Quantitative Data*. John Wiley & Sons, New York.

Vasiliauskas, S.A. & Aarssen, L.W. (1992) Sex ratio and neighbor effects in monospecific stands of *Juniperus virginiana*. *Ecology*, **73**, 622–632.

Van Uden, S., Stewart, G.H. & Duncan, R.P. (1998) Implications of dioecy for sustainable forest management. *New Zealand Forestry*, **42**, 39–42.

Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **22**, 1–22.

Waser, N.M. (1984) Sex ratio variation in populations of a dioecious desert perennial, *Simmondsia chinensis*. *Oikos*, **42**, 343–348.

Weiner, J. (1984) Neighbourhood interference amongst *Pinus rigida* individuals. *Journal of Ecology*, **72**, 183–195.

Weiner, J. & Thomas, S.C. (1986) Size variability and competition in plant monocultures. *Oikos*, **47**, 211–222.

West, P.W. (1984) Inter-tree competition and small-scale pattern in monoculture of *Eucalyptus obliqua* L'Herit. *Australian Journal of Ecology*, **9**, 405–411.

Williamson, G.B. (1975) Pattern and seral composition in an old-growth beech-maple forest. *Ecology*, **56**, 727–731.

White, P.S. & Pickett, S.T.A. (1985) Natural disturbance and patch dynamics: an introduction. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 3–13. Academic Press, New York.

Whittaker, R. H. (1965) Dominance and diversity in land plant communities. *Science*, **147**, 250–260.

Whittaker, R. H. (1970) *Communities and Ecosystems*. The Macmillan Company, London.

Woods, K.D. (1984) Patterns of tree replacement: canopy effects on understory pattern in hemlock - northern hardwood forests. *Vegetatio*, **56**, 87–107.

Yamamoto, S. (1989) Gap dynamics in climax Fagus crenata forests. *Botanical*

Magazine, *Tokyo*, **102**, 92–114.

amamoto, S. (1992) Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. *Botanical Magazine*, *Tokyo*, **105**, 29–45.